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LIMNOLOGY OF THE LOWER MISSOURI RIVER[1, 2]

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INTRODUCTION

This paper presents limnological data from the Missouri River and, whenever possible, compares the Missouri River with the other major rivers of the United States.

Most of the data presented were collected by the writer[3] as a member of the Missouri Conservation Commission crew which conducted a fisheries and limnological survey of the lower Missouri River from April 12 through October 31, 1945. The limnological phase of this work was considered important, for with the exception of the Illinois River, there have been few thorough limnological investigations of the larger rivers of this country.

Clarke (1924) compiled the scattered records on the chemical composition of the rivers of the United States. Since then Platner's (1946) paper on the upper Mississippi River has been the major publication on river chemistry. This study revealed that on the whole the chemical characteristics of this river were not seriously detrimental to the aquatic life therein, but that in local areas below particular industrial plants and cities the pollutants did produce such detrimental conditions.

Plankton studies have been more numerous, but no complete studies have been published on the large, highly turbid rivers. Kofoid (1903, 1908) found that most of the plankton in the Illinois River had originated in the lakes and backwaters associated with it, and that none of the plankters were characteristic of the river itself. Allen (1920) noted a decrease in plankton with an increase in the current of the San Joaquin River. In the upper Mississippi River, Galtsoff (1924) found that Lake Keokuk, an artificial impoundment, and the natural river-lakes harbor a richer plankton population than does the river itself. Ellis (1931) found the plankton population of Lake Keokuk to be much lower than that reported by Galtsoff a few years earlier and suggested the recent reduction of the littoral zone as an explanation.

Similarly, the studies of the benthic productivity of rivers have been largely limited to the smaller, less-turbid streams. Richardson (1921a, 1921b, 1928), in addition to his conclusions regarding the changes associated with pollution, found that the benthos varied inversely with the

[1] Contribution from the Missouri Cooperative Wildlife Research Unit, United States Fish and Wildlife Service, Wildlife Management Institute, Missouri Conservation Commission, Edward K. Love Foundation, and the University of Missouri cooperating.

[2] Condensed from the thesis, "A limnological survey of the Missouri River from its mouth to the Iowa State line during the summer of 1945," filed in the Library of the University of Missouri, Columbia, Missouri, 1947.

[3] The writer is indebted to many people for assistance in the preparation of the thesis and in the field, but he especially wishes to express his appreciation to the following: Mr. E. K. Love, who established the fellowship which supported this study; Dr. Robert S. Campbell of the University of Missouri for the direction of the research; and to Dr. G. B. Herndon of the Missouri Conservation Commission for advice and equipment.

current velocity and directly with the amount of vegetation. Most of the studies of the benthos in the Mississippi have been in Lake Keokuk (Ellis 1931) or in the polluted area below St. Paul (Wiebe 1930).

Comparatively little work has been done with that group of organisms referred to by other workers as the "drifters" or "drifting organisms," but referred to in this paper as the syrton (sur'ton). (The term "syrton" was coined from the root of the Greek word *συρτων συρν*, to draw or to drift.) Syrton, as herein employed, is defined as a heterogeneous, macroscopic group of living and dead organisms including all of the aquatic and terrestrial insects, other invertebrates, and the small fishes being carried by the current on or below the surface of the water.

A number of limnologists have studied benthic organisms in relation to floods, and most of them have left the impression that the occurrence of aquatic organisms in the current of any stream was unnatural. Dendy (1944) was probably the first to recognize the naturalness of this drifting. He wrote,

"Although drifting may not be a normal event in the life of the individual animal, the occurrence of aquatic animals in the drift in the three streams studied is natural, even though the streams are not subject to flooding."

Investigations of the fishes of the larger rivers have been largely confined to the commercial species and their harvest. Thompson (1931) calculated that the annual yield of fishes from the Illinois River and its associated lakes varied from four to twenty-four million pounds during the years from 1896 to 1922. Forbes and Richardson (1919) described the changing species composition in the Illinois River in relation to the degree of pollution. Coker (1930) concluded that the more important game and commercial fishes of the Mississippi River may have been benefited by the Keokuk Dam. In Keokuk Lake the game fishing remained good until the shallow littoral areas were destroyed (Ellis 1931).

Description of the Missouri River

The Missouri River is 2,600 miles long and drains about 529,000 square miles, almost 1/6 of the total area of the United States. Its average discharge was about 59,000 cubic feet per second during the 11 year period from 1928 to 1939 (Beckman 1940). This is about 1/2 that of the upper Mississippi, about 1/4 that of the Ohio, but is about 3 times that of the Colorado or the Illinois Rivers. The mean current velocities in the lower Missouri range from 2 to 7 miles per hour (U. S. Army Corps of Engineers 1946). Forbes and Richardson (1920) gave the velocity of the Illinois River during its nearly normal stages as between 1½ and 2½ miles per hour. On the other hand, the Colorado River has a current velocity even greater than that of the Missouri.

Gravel and coarse sand cover most of the river bottom. Finer sand, often almost free of mud, is found on the inside of the bends. For a few yards below the pile dikes and along the steep gumbo banks there is usually a deposit of a silty ooze.

No rooted aquatic plants were found in the channel, chutes, or backwaters of the Missouri River.

During the flood periods, two of the tributaries which enter the lower Missouri River, the Grand and Osage Rivers, frequently have a pronounced effect upon the stage of the Missouri River. Furthermore, whenever the level of any tributary is well above that of the Missouri, a considerable number of aquatic organisms are discharged into the main river.

As a result of the work for the improvement of river navigation, the Missouri River now has very few associated lakes and backwaters. In contrast, the Mississippi (Ellis 1931), Illinois (Forbes and Richardson 1920), and the Colorado (Dill 1944) were described as having a considerable number of lentic habitats.

A concise description of the Missouri

River before and after the work of the United States Army Corps of Engineers (1946), reads as follows:

"Prior to improvement by the Corps of Engineers, the river meandered through the valley and it has not been uncommon for the wild river to erode and carry away a whole farm in the course of a day or, by avulsion, to shift several farms from one side of the river to the other. Between the rock bluffs the river in its natural state built itself high banks, easily erodible, which contained the normal high water but were overtopped by floods. These banks were from 1,500 feet to a mile apart, covered with willows, cottonwoods, and hardwoods. In general, the river followed a meandering course of bends and reaches impeded by soft and shifting bars, shoals, snags, and debris which frequently caused the formation of two or more shallow channels. Smoothly-curved bends in a single fixed channel now characterize the river after improvement work. The river is no longer uncontrolled and the danger that large areas of farm land might be eroded overnight has been eliminated almost entirely."

To control the river the engineers are using the revetments and permeable pile dikes described in the pamphlet quoted above. The pile dikes give the current the proper direction, and the revetments stabilize the banks. The pile dikes have a second function. As the river with its load of silt flows through the dikes, flotsam accumulates on the upstream sides of the dikes, and the velocity of the current is reduced enough to bring about the deposition of silt. Thus many areas that originally were often covered with shallow water are now covered with several feet of silt and a thick growth of willows.

There are no data concerning the effect of untreated domestic and industrial wastes which are allowed to enter the Missouri River on the aquatic life therein. Neither are there comparative data regarding differences in the amount of erosion silt in the river before and since the advent of the plow.

Methods

At each of the 11 work stations (sections of the river about 5 miles long) a limnological series was obtained from each of the 4 major type-sites: the middle of the channel, near a steep bank, near a sand bar, and the down-stream side of a pile dike. Whenever time permitted, additional studies were made in adjacent waters.

Each complete limnological series included temperature and total turbidity readings; pH, dissolved oxygen, acidity, and alkalinity determinations; collections of minnows and small fishes, digestive tracts of several mature fishes, benthos, plankton, and syrton. Unless otherwise stated, the procedures used for all chemical determinations, were those described in "Standard methods for examination of water and sewage" (Amer. Pub. Health Assn. 1936). The Rideal-Stewart modification of the Winkler method was selected for the oxygen determinations.

Physical and Chemical Characteristics

Temperature

During the period of the study from mid April through October, 1945, the water temperatures ranged from 46 to 82° F, but temperatures of 32° F are common during the winter. During the last half of July and the first half of August the average water temperature was about 79° F. Surface and bottom temperatures differed less than 1° F.

Total turbidity

Turbidity is perhaps the most important single factor limiting aquatic life in the Missouri River (Ellis 1937). Comparatively few species can withstand the conditions usually associated with high turbidities, i.e., sedimentation, low light intensities, interference with respiration and other physiological processes, and higher water temperatures. Furthermore, as is explained below under the heading, "Dissolved Oxygen," the amount of dis-

solved oxygen in this portion of the Missouri River varies inversely with the turbidity.

During the high water period of 1945, which ended about August 15, the average turbidity, as determined by a U. S. Geological Survey turbidity rod, was about 4,500 ppm, but several of the readings were as high as 8,000 ppm. After August 15 the turbidity averaged about 1,700 ppm.

Platner (1946) reported that the average turbidity of the Mississippi River just above the mouth of the Missouri River was about 300 ppm, whereas below the mouth of the Missouri River the average jumped to 1,880 ppm. September readings of the Secchi disk in the upper Mississippi River (Galtsoff 1924) ranged from 3 to 32 inches. In the Missouri River this disk often disappeared at ½ inch.

Hydrogen-ion concentration

The hydrogen-ion concentration in the channel varied from pH of 7.4 to 7.8. Single determinations of pH 7.2 and 7.9 were the only exceptions. These values fall within the range pH 6.0 to 8.7 which Ellis and his co-workers (1946) considered indicative of conditions not unfavorable to fish. The pH readings in the Missouri River were obtained by using a Hellige Pocket Comparator with phenol red as the indicator. All readings had to be made while facing the best source of light because of the high turbidities encountered; but, even with this modification of the usual practice, accurate pH determinations could not be obtained in a tributary which maintained a turbidity of about 15,000 ppm for several days.

Platner (1946) found that the Mississippi below the mouth of the Missouri River had an average of pH 7.90 ". . . whereas in the upper section it was 8.25."

Free carbon dioxide

Free carbon dioxide was found in amounts varying from 1 to 10 ppm as determined by the titration method using N/44 sodium hydroxide. By the use of Moore's (1939) nomograph, which is based upon the relationship that exists between the total carbonates, the pH, and the free carbon dioxide, the free carbon dioxide was found to vary from 2.12 to 7.70 ppm.

In 1944 Platner (1946) found free carbon dioxide present in amounts no greater than 1 ppm in the Mississippi River and only as traces in the mouth of the Missouri River.

Carbonates and bicarbonates

No normal carbonates were detected in the Missouri River, but concentrations of bicarbonates ranging from 83 to 185 ppm were measured. In the Mississippi River, Platner (1946) measured concentrations of bicarbonates that varied from 51 to 112 ppm. Occasionally he found small amounts of normal carbonates.

Dissolved oxygen

During the survey, the dissolved oxygen content of the Missouri River ranged from 3.5 to 9.9 ppm. Dissolved oxygen concentrations as low as 3.5 ppm may be too low for the well-being of the fish and may be one of the factors limiting the species in the Missouri River. Ellis and his co-workers (1946) have stated that a varied fish fauna can be expected only in waters with a dissolved oxygen content that is above 5 ppm. They also state that asphyxia can be expected if the dissolved oxygen content of the water drops lower than 3 ppm in waters of 25° C. The Missouri River always had more than 3 ppm of dissolved oxygen, but the water temperature occasionally rose to 28° C.

Unpolluted running waters are normally well supplied with dissolved oxygen. On March 13 when the Missouri was relatively clear, its oxygen content was about 95 per cent of saturation. In contrast, saturation values of less than 50 per cent were common during the summer. This was especially true during the highly turbid, high water period of early August. Waters of the same temperature

but collected during the less-turbid, low water period were more highly saturated with dissolved oxygen. This suggests that the oxidation of the organic fraction of the material producing the turbidity may have been responsible for the dangerously low oxygen level. Platner (1946) made a similar suggestion regarding the Mississippi.

Biological Characteristics

Net plankton

Usually, 23.5 liters of river water were strained for a sample of plankton. Since a cubic centimeter of silt was commonly and unavoidably collected with the plankton, a sedimentation-decantation technique was used to separate the silt from the plankton. This method consisted of diluting the sample to 100 ml in a color-comparison tube which measured 16 cm from the 100 ml mark to the bottom of the tube, shaking the sample, and allowing it to settle for three minutes before the top 14 cm were siphoned into a plankton-net barrel which was partially immersed in water. After ten repetitions of this dilution-sedimentation-decantation process, the material collected in the barrel was examined microscopically. This method was about 95 per cent efficient; the greatest losses occurred among the longer strands of filamentous algae and the large, heavier zooplankters.

During the 7 months of the survey, the Missouri River plankton population averaged 67.4 individuals per liter of water or 67,400 per cubic meter. Based on the average of 52 weekly collections, Kofoid (1908) found about 647,700,000 plankters per cubic meter of the Illinois River which at that time was connected with many lakes and backwaters. Kofoid included many bacteria and protozoa in his counts, but even if these groups are excluded his counts were still about 400,000,000 per cubic meter. Allen (1920) reported that in 1913 the plankton population of the San Joaquin River averaged about 50,000,000 individuals per cubic meter.

The paucity of the plankton in the Missouri River is probably the result of this river's (1) turbidity, (2) high current velocity (Welch 1935) and (3) its lack of adjoining lentic environments (Kofoid 1908).

Apparently, however, conditions were not always unfavorable for all species, for two phytoplankton pulses were noted. *Pediastrum* was responsible for the first pulse. This pulse reached its peak about the middle of July and had run its entire course in a little more than two weeks. The second pulse, which reached its peak during the second week of October, was due primarily to *Fragilaria*. *Asterionella* and other diatoms showed slight increases. Although still unusually high, the diatom population had decreased by the end of the month when the survey ended.

Table I presents the composition of the plankton in the Missouri River.

Table I. *Composition of the Missouri River plankton April through October 1945*

Plankton group	Composition of 34 collections (per cent)
Myxophyceae	
Colonial	0.19
Filamentous	1.31
Bacillarieae	
Fragilaria	22.62
Asterionella	2.69
Other	1.15
Chlorophyceae	
Eudorina (?)	1.41
Filamentous	5.09
Pediastrum	25.67
Desmidiaceae	0.30
Dinophyceae	
Ceratium	1.37
Other algae (unidentified)	
Colonial	0.29
Filamentous	2.37
Protozoa	3.63
Nematoda	15.99
Rotifera	7.05
Cladocera	0.18
Copepoda	1.03
Nauplii	6.71
Acarina	0.19
Tardigrada	0.05
Insecta	
Mature	0.17
Immature	0.19
Eggs and cysts	0.36
Total phytoplankton	65.00
Total zooplankton	35.00

The two most common phytoplankters, *Fragilaria* and *Pediastrum*, amounted to 23 and 26 per cent of the total plankton, respectively. In addition to exhibiting a pulse, *Pediastrum* was common throughout the study period whereas *Fragilaria* was practically absent until the October pulse.

Nematodes, referred to by Kofoid (1908) as adventitious plankters, made up about 16 per cent of the total plankton in the Missouri River. Although rarely in large numbers, they appeared in 32 of the 34 collections. The second and third most abundant zooplankters, the rotifers and the nauplii, occurred in 31 of the 34 samples.

If all of the plankton collections are considered, the phytoplankton-zooplankton ratio was about 2:1. If only those collections not affected by the relatively short phytoplankton pulses are considered, this ratio is reduced to 44:56. In comparison, Kofoid (1908) reported a 5:1 ratio for the Illinois River, and Allen (1920) reported ratios of 2.5:1, 9:1, and 9:1 for the three stations in or associated with the San Joaquin River. The lower phytoplankton-zooplankton ratio found in the Missouri River is probably another effect of the turbidity.

Much of the Missouri River plankton must be autochthonus, for neither the Missouri River itself nor its tributaries are closely connected with lentic environments. Only when the flood waters cover the weedy and woody areas outside of the river channel does the Missouri River have waters which are slightly more productive than the river proper.

Benthos

About 1/5 of a square meter of the river bottom was sampled with a Petersen dredge for each collection of benthos. The silt-like fraction of these collections was removed with a screen. If almost all of the retained material was sand or gravel, the calcium chloride flotation treatment was applied before the material was hand sorted.

TABLE II. *Productivity of the benthos in the several type-sites in the Missouri River*

Type-site	Number of hauls with dredge	Weight of organisms in pounds per acre		
		Aquatic	Terrestrial	Total
Near middle	8	0.01	0.20	0.21
Near a steep bank	60	2.17	0.12	2.29
Near a sand bar	29	0.67	1.42	2.08
Downstream from a pile dyke	30	1.27	0.03	1.30

A 50 mg capacity precision balance was used to obtain the moist weight of each of the benthic collections. These weights, presented in table II, are probably only 80 per cent of the original weights, since the organisms had been preserved in alcohol from 12 to 18 months before they were weighed (Richardson 1921a).

Within the Missouri River the areas most productive of a true benthos were near the steep banks, but even these areas averaged only 2.17 pounds per acre. The areas downstream from the pile dikes supported about 1.27 pounds per acre. The channel itself and the sites near the sand bars yielded only 0.01 and 0.67 pounds per acre, respectively. The channel probably does not produce any benthic organisms. The one *bezzia* larva taken may have been drifting in the current.

In 1945 the Missouri River produced less than 0.4 of a pound of true benthic organisms per acre (0.40 kg per ha). Even if the terrestrial organisms were included, the total available benthic food was less than 0.7 of a pound per acre (0.73 kg per ha).

Of the Illinois River between Chillicothe and Grafton, Richardson (1921a) wrote, "The general average for the river channel from Chillicothe to the mouth was 261 pounds per acre." Richardson reported many counts of between 200 and 400 aquatic organisms per square yard. Some of his counts ran over 3,000 per square yard. At the time of his study and on the basis of 300 per square yard there must have been about 1,452,000 benthic organisms per acre in the Illinois

River as compared with 80,000 per acre in the Missouri River in 1945.

The paucity of benthos in the Missouri River is undoubtedly due to environmental features which other workers have associated with low productivity in other waters. These features are: shifting substratum (Eggleton 1939); siltation (Gersbacher 1937 and Ellis 1931); fluctuating water level (Ellis 1931); swift current (Eggleton 1939, Hora 1930, and Luce 1933); and the absence of aquatic vegetation (Richardson 1921a).

Table III gives the composition of the benthos in the Missouri River, but it also

TABLE III. *Species composition of the Missouri River benthos*

(Based on 750 organisms found in 130 Petersen dredge hauls collected from April through October, 1945)

Benthic group	Per cent of total organisms found	
Diptera		
Chironomidae		
Larvae	34.9	
Pupae	0.3	
Chaoborus larvae	4.1	
Bezzia larvae	3.1	
Other immature Diptera	4.0	
(Total immature Diptera)		(46.4)
Plecoptera	3.2	
Ephemerida	3.2	
Odonata	2.0	
Trichoptera	16.5	
(Total aquatic Insecta)		(71.3)
Aquatic Annelida	19.9	
Other aquatic organisms	0.7	
(Total aquatic organisms)		(91.9)
Terrestrial organisms and Notonectidae	8.1	
Total of all organisms	100.0	

includes the terrestrial organisms and does not, therefore, give the composition of the benthos as it is usually considered. These terrestrial organisms must be important in the ecology of the river since they make up about 45 per cent of the weight of the organisms collected and they are found in the stomachs of many fishes.

Almost half of the organisms taken were the larvae of Diptera. Thirty-five per cent were the larvae of Chironomidae, and about 8 per cent were terrestrial organisms.

During the period of the study there were distinct fluctuations in the abundance of Plecoptera nymphs and *Chaoborus* larvae. Insufficient sampling and station differences may have been responsible for the fluctuations or the lack of fluctuations observed in the other insect groups.

The Plecoptera nymphs were common during the early part of the survey but their numbers decreased as the season advanced. None were taken from June 23 to October 26 although the freshwater sheepshead were able to find a few during this period. Almost all of the *Chaoborus* larvae were taken from August 19 to September 25. Only on August 19 and 20 were the *Chaoborus* pupae found.

No clams, snails, or crayfish were found in the dredge samples. The crayfish found in the stomach of some of the fish probably had been staying in or under the unsampled flotsam associated with the pile dikes.

Syrton

In order to sample the syrton of the Missouri River a bobbinet-cloth cone 4 feet long and with a 0.5 square-foot mouth was placed in the water with its open end upstream. To calculate the volume of water strained it was essential to know the velocity of the current, the length of time the net was collecting, and the slip-stream loss factor.

Fifty-four collections of syrton were obtained during the 6 months, May through October of 1945. During 1946, 22 additional samples were collected to obtain a clearer picture of the vertical distribution of the syrton.

As is shown in table IV, the benthos and syrton are similar not only as to species composition but also, with a few exceptions, as to the relative abundance of the different species. For example, the chironimid larvae dominate numerically both the benthos and the syrton, while the numbers of all other immature Diptera in both populations are comparatively insignificant. The Trichoptera larvae are

TABLE IV. *Species composition of the benthos and of the surface syrton in the Missouri River from May 9 through October, 1945*

Organisms	Benthos (per cent of 629 organisms)		Syrton (per cent of 381 organisms)	
Diptera				
Chironomidae larvae	31.3		45.9	
Chironomidae pupae	0.2		2.6	
Chaoborus larvae	4.8		2.9	
Chaoborus pupae	0.0		1.6	
Bezzia larvae	2.4		0.3	
Other immature Diptera	4.5		0.3	
(Total immature Diptera)		(43.2)		(53.6)
Plecoptera nymphs	2.5		9.4	
Ephemerida nymphs	3.0		11.5	
Odonata nymphs	1.9		0.5	
Trichoptera larvae	19.1		12.1	
(Total aquatic Insecta)		(69.7)		(87.1)
Aquatic annelida	21.1		0.5	
Other aquatic organisms	0.8		1.1	
(Total benthic organisms)		(91.6)		(88.7)
Terrestrial organisms	8.4		11.3	
Total of all organisms	100.0		100.0	

common in both, and even the terrestrial organisms are present in about the same percentage in each population. In contrast, these populations are dissimilar in reference to the relative abundance of the Annelida and the Plecoptera and Ephemerida nymphs. The annelids formed 21.1 per cent of the benthos but only 0.5 per cent of the syrton; in contrast, the Plecoptera nymphs made up only 2.5 per cent of the benthos but 9.4 per cent of the syrton. Likewise, the Ephemerida nymphs accounted for only 3.0 per cent of the benthos but 11.5 per cent of the syrton. From these benthic-syrtonic ratios it appears that the annelids which tunnel in the bottom muds are less likely to become members of the syrton, and, therefore, may be considered better fitted for life in the Missouri River than are the nymphs which cling to debris that may be dislodged by the turbulent river.

The abundance and vertical distribution of the syrton tends to parallel that of the plant debris. The syrton and plant debris were always more abundant near the bottom than at intermediate depths, but when sharp rises in the river level greatly increased the amount of surface debris, the syrton became more abundant on the surface than at any other level.

On April 18, 1946, in spite of the fact that there was very little surface debris on the Missouri River it was estimated that more than 64,000,000 organisms weighing about 450 pounds passed under the Boonville bridge in 24 hours. This represented a population of 0.068 pounds per surface acre, which was equivalent to 10 per cent of the standing crop of benthos in 1945.

The syrton may be important to the fishes of the Missouri River as a source of food and as a quick source of reseeding stock for those areas recently deposited.

Pile-dike fauna

In the Missouri River the debris that collects on the upstream side of the pile dikes tends to fulfill, in some respects, the role played by aquatic plants in other waters. Richardson (1921a) pointed out that plants usually increase the productivity of aquatic environments. Hubbs (1932) suggested a similar role for debris when he observed that "insects hatch and crawl about on this material in great quantity."

No techniques were developed to sample quantitatively the fauna on and under this debris, but the immature stoneflies, mayflies, and caddisflies were common thereon. Crayfish were found in the stomachs of fishes, and, since they were not taken in the bottom samples, it is assumed that they live under the debris.

Little is known concerning the fish fauna of the pile dikes and its debris, but the results of seining suggest that the half-grown fishes are more abundant around the pile dikes. Since these pile dikes are almost the only hiding and resting places in the river, the mature fishes, especially the nocturnal catfishes, must also use them. Moreover, if the catfishes spawn in the river, they must use the debris associated with the pile dikes for holes such as they prefer would be rare elsewhere.

TABLE V. *Species composition of catch of commercial fishes in the Lower Missouri, in the Mississippi River along the State of Missouri and in the Missouri-Illinois-Iowa section of the Mississippi River in 1945*

(Expressed as percentages of the total catch by weight)

Species	State of Missouri		Missouri-Illinois-Iowa section of the Mississippi River
	Missouri River	Mississippi River	
Carp (*Cyprinus carpio*)	59.2	43.2	41.9
Buffalofishes			
Big-mouth (*Megastomatobus cyprinella*)			
Small-mouth (*Ictiobus bubalus*)	17.0*	19.7	24.4
Mongrel (*Ictiobus niger*)			
Sheepshead (*Aplodinotus grunniens*)	4.0	14.9	13.3
Quillback (*Carpioides* spp.)	—	1.5	1.8
Sucker (*Catostomidae*)	1.3**	0.3	0.8
Catfishes			
Flathead (*Pilodictis olivaris*)			
Channel (*Ictalurus lacustris*)	13.4†	15.9	14.0
Blue (*I. furcatus*)			
Sturgeon (*Acipenseridae*)	1.3	1.0	0.6
Bullhead (*Ameiurus* spp.)	0.2	0.6	1.3
Dogfish (*Amia calva*)	—	0.1	0.5
Gar (*Lepisosteus* spp.)	2.4	1.3	0.2
Eel (*Anquilla bostoniensis*)	0.1	0.2	trace
Mooneye (*Hiodon tergisus*)	—	—	0.1
Paddlefish (*Polyodon spathula*)	—	1.3	0.3
Northern pike (*Esox lucius*)	—††	—	0.1
Turtle	—	—	0.1
Miscellaneous	—	—	0.5

* Roughly about 70 per cent big-mouth buffalofish, 29 per cent small-mouth buffalofish, and 1 per cent mongrel buffalofish.

** Most of the fishes classified as suckers were quillbacks.

† Flathead catfish 11.5 per cent and channel catfish 1.9 per cent. The rare blue cat or Fulton was recorded with the channel catfish.

†† Not a commercial species in Missouri.

Fishes

The composition of the commercial catch of fishes from the Missouri River (Missouri Conservation Commission, unpublished) and comparable data from the Mississippi River (Upper Mississippi Conservation Committee, unpublished) are given in table V.

In general the same species are found in the commercial catches of both waters. Based upon test fishing the carp and gar are relatively more abundant in the Missouri than in the Mississippi while the buffalofishes and sheepshead are less abundant.

The commercial fishery, as well as test fishing with small meshnets and seines, emphasizes the almost total absence of the fine or game fish. Sixty per cent of the almost 16,000 small fishes collected from the Missouri River with a ¼ mesh seine consisted of the minnow, *Hybognathus.* Another minnow, *Platygobio gracilis,* accounted for another 30 per cent of the small fishes. About 9 per cent of the small fishes were the young of commercial species, and of these more than 75 per cent belonged to the Catostomidae. About 0.4 per cent of the small fishes were the young of Centrarchidae, the adults of which were rarely taken in the 2½ inch bar-measure commercial nets.

A more detailed analysis of the small fish collections and data on the spawning, sex and age ratios, and the growth rates of the commercial species are on file with the Missouri Conservation Commission.

Fish foods

The contents of the stomach or upper intestinal tract of 143 mature fishes of 7

species of commercial importance were analyzed.

The food habits of the carp and the small-mouth buffalofish were similar with diets of plant debris, 43 and 32 per cent, respectively, and plant seeds, 29 and 59 per cent respectively. The food habits of the big-mouth buffalofish and the quillback were also similar in that microfauna formed a big percentage of the material ingested by both species. The sheepshead were strictly meat eaters. They had ingested fish (36 per cent), crayfish (25 per cent), and aquatic insects (31 per cent). The catfishes, especially the channel catfishes, were somewhat more omnivorous than the sheepshead, but crayfish and fish were the most important foods ingested.

TABLE VI. *A composite of the foods ingested by the commercially important fishes* of the Missouri River*

Food group	Per cent of total volume
Plant debris	33.2
Plant seeds	20.8
Microfauna	10.2
Aquatic insects	8.1
Terrestrial insects	5.3
Crayfish	6.4
Fish	13.8
Miscellaneous	2.2

* Big-mouth buffalofish, small-mouth buffalofish, quillback, carp, channel catfish, flathead catfish, and sheepshead (for the scientific names, see table V).

In order to present collectively the feeding habits of the commercially important fishes of the Missouri River (table VI) the different items ingested by each species were weighted in accordance with the relative abundance of the species in which they were found. This composite emphasizes the bottom feeding habits of the Missouri River fishes. It also emphasizes the importance of allochthonous organic matter in the Missouri River ecosystem, for 54 per cent of the foods ingested, namely plant debris and seeds, originated beyond the river. Digestion coefficient studies were not conducted, but much of this organic matter, especially the seeds, must be digestible.

Discussion

Directly or indirectly every limnological feature of the Missouri River is conditioned by its very high turbidity. This turbidity and the characteristics of the river which promote turbidity (high current velocity, shifting substratum, and others) are largely responsible for the paucity or total absence of many biotic forms.

Probably because of the turbidity, the basic productivity of the Missouri River is very low. In most clear waters aquatic plants are present which convert and store radiant energy thereby compensating for the energy losses concomitant to the transfer of energy from one trophic level to another. In contrast, in the Missouri River allochthonous detritus is used to compensate for such losses because this river has no phanerogams and relatively few phytoplankters.

Since every trophic level in the Missouri River utilizes allochthonous organic matter, the net plankton and the benthos have reduced values as indices to productivity. For example, the standing crop of benthos, including the dead terrestrial organisms but excluding the unmeasured pile-dike fauna, averaged less than ¾ of a pound per acre, but the fish harvest amounted to about 10 pounds per acre. Presumably the fishes derive much of their energy from terrestrial plant debris and seeds.

A relatively high current velocity was responsible for the presence of syrton, i.e., the drifting organisms. Quantitative and distributional changes in the syrton and drifting plant debris are parallel, and such changes are usually brought about by variations in the river stage. This syrton may be of importance to the river fishes directly as a source of food and indirectly as seedstock to repopulate areas of recently deposited silt.

Summary

The turbidity, which commonly was greater than 3,000 ppm, affected almost

every characteristic of the lower Missouri River. The water temperature rose to a high of 82° F. The oxidation of the organic fraction of the material producing the turbidity may have been partially responsible for the mid-summer dissolved oxygen saturation values of less than 50 per cent. The lowest dissolved oxygen concentration found was 3.5 ppm.

Usually, probably because of the turbidity, the phytoplankters were less common than the zooplankters. However, the phytoplankton : zooplankton ratio for the April through October period was about 2 : 1 because of a July *Pediastrum* pulse and an October *Fragilaria* pulse. The plankton population averaged only 67 individuals per liter.

The factors largely responsible for the turbidity, a mean current velocity of 2 to 7 mph and a shifting substratum, probably were responsible for the paucity of benthos which, dominated by Chironomidae, averaged less than 0.4 pounds per acre. Furthermore, these factors were largely responsible for the syrton (an assemblage of drifting organisms similar in species composition to the benthos) which averaged almost 0.07 pounds per surface acre.

A rough-fish population, composed chiefly of carp, buffalofishes, and catfishes, annually yielded to the commercial fishermen about 10 pounds per acre. More than half of the foods ingested by these "taste and feel" feeders was of allochthonous plant origin.

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SOME FACTORS AFFECTING THE ABUNDANCE OF MINNOWS IN THE DES MOINES RIVER, IOWA [1]

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INTRODUCTION

In all types of waters, fish populations appear to fluctuate in abundance and in species composition from year to year. The causes of these fluctuations and the effects of environmental and biological forces upon them are for the most part unknown. Since most minnows (Cyprinidae) are short-lived fishes and are abundant even in relatively small areas, they are especially valuable for population dynamics studies. The effect of various factors on a minnow population can be detected within a few years, whereas many years would be required to make similar observations on longer-lived game or commercial fishes.

The present investigation deals with changes in the minnow populations of a stretch of the Des Moines River, Boone County, Iowa, from 1946 through 1948. A marked difference in the abundance of various species of minnows was noted and, as will be shown later, high water or flood stages appear to explain several of the changes. The availability of space and the population density of the minnows appear to modify the abundance under certain conditions. Most of the species of minnows found abundantly in the river are absent from the smaller tributary streams. It has already been pointed out (Starrett, 1950a) that some of these differences in distribution are associated with ecological preference, tolerance of other species, and hardiness to conditions associated with drying and isolation of pools. The scarcity of entomostraca in the river during late spring and summer was also found to be a possible limiting factor for species that normally feed either as young or as adults upon these microcrustacean organisms (Starrett 1950b).

RESEARCH AREA

The Des Moines River is typical of other medium to large midwestern rivers in many respects. The watershed is large and 93 per cent of it is farmed (U. S. 71st Congress, 3rd Session, 1931). The river is subject to fast rises after heavy rains. Floods are more common in May and June than at any other time of the year, since the heaviest precipitation normally occurs during these months. Cloudbursts and heavy rains occasionally cause local temporary floods in summer and floods are not uncommon in early fall. Frequently an early spring flood follows thawing and fast run-off of the water. The silt load of the river increases with a rise in water levels. Silt was the only type of pollution noted in the river.

This investigation was limited to the Des Moines River and other streams in Boone County, Iowa. Boone County is about midway in the course of the Des Moines River. Fish were collected at 17 places on the Des Moines River, but most of the detailed studies were made at 3 stations, described as follows:

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TABLE I. *Number of days on which river stage was over 1.49 feet for May through September, 1933–1948, Des Moines River at Boone, Iowa*

Month	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	No. years water less than 1.5 ft.
May	6	0	0	5	19	28	0	0	1	22	12	31	31	11	30	11	4
June	2	4	12	2	24	18	0	0	22	23	18	30	30	21	30	0	3
July	3	0	10	0	0	20	0	0	4	14	29	23	11	6	21	0	6
August	23	0	0	0	3	12	0	6	0	14	25	0	12	0	0	0	9
September	12	0	0	7	0	23	0	0	6	21	5	0	0	0	0	0	10

Station 1 (T-85 N, R-27 W, Sec. 27) was established 2 miles above a lowhead dam at Fraser.

Station 2 (T-84, R-27 W, Sec. 2) at the Fraser lowhead dam was selected for the principal studies because of accessibility for seining operations.

Station 3 (T-83 N, R-26 W, Sec. 18) was near the town of Moingoina, 16.8 miles below Station 2.

Further descriptions of the area are given in other papers (Starrett 1950a, 1950b).

River Stages

The river stages recorded daily at the Boone Water Works (near Station 2) between 1933 and 1947 are averaged and presented graphically in Figure 1. The graph includes only the monthly averages during the spawning seasons of the minnows. Through this 15-year period, river stages averaged higher and remained high for longer periods in May and June than in any of the other months. The average tended to be lower in July and at the minimum in August and September. The 1945 and 1946 river stages are plotted separately on the graph for comparison. Water levels in 1945 were above normal throughout the summer, while they were below normal in 1946. The high water in August 1945, as will be discussed later, appears to have been particularly significant to the minnow population. A summary of the number of days in each month during the 16-year period of 1933 through 1948 when the river exceeded 1.49 feet is given in Table I. The river stage of 1.49 feet was determined as estimated maximum stage favorable for minnow spawning. Successful spawning of several species of minnows occurred below this stage following high-river stages in the summers of 1946 and 1947. This successful spawning was associated with less turbid waters and higher production of bottom ooze and phytoplankton than existed during high-river stages. Water levels above the 1.49 feet stage are accompanied by turbid water, fluctuating levels, and reduction in bottom ooze and phytoplankton. If the river remained constantly at a stage above 1.49 feet throughout the summer without a heavy silt load, perhaps very favorable conditions for spawning would develop. Such a condition would provide more space, a factor that appears to be very important in the successful spawning of Des Moines River minnows.

Table I indicates that high water does occur some years in August and September but less frequently than in the spring months. In June 1948, the average river stage was 0.68 feet as compared to averages of over 5 feet in 1945 and 1947 (Table II). In July 1947, there were 11 days on which the river stage was 5 feet

TABLE II. *Monthly average river stages, in feet, of Des Moines River at Boone Water Works during spawning seasons of 1945 through 1948*

Month	Year			
	1945	1946	1947	1948
May	4.08	2.80	2.19	1.33
June	5.97	2.70	7.41	0.68
July	1.59	1.22	4.50	0.71
August	2.44	0.54	0.62	0.50

or more. The flooding stage was not reached again during the remainder of 1947 and 1948.

Following a heavy rain the Des Moines River often will rise locally within a few hours. On the morning of June 23, 1947, the river stage at the Boone Water Works was 8.60 feet and within the following 24 hours the river rose to 16.60 feet. The fall or recession of the river is much slower than the rise, usually less than a foot per day. The most rapid fall appears to occur when the river is about 10 feet, and at this stage it may drop more than 2 feet per day. Seining operations indicated that minnows as well as other fish move into the shallow backwater areas created by floods. Coker (1914) mentions that during high water on the Mississippi River spawning grounds may be found some distance from the main course of the river, and that an untimely recession will leave a generation of young fish isolated in some overflow and left for destruction unless rescued. In 1947 observations were made of such isolated populations along the Des Moines River following a flood. The minnow population left to die in isolated temporary backwaters was found to be large. Seine hauls produced thousands of minnows, some black bullheads, *Ameiurus melas melas* (Rafinesque); a few carp; carpsuckers, *Carpiodes* spp.; and young yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill). The minnow population isolated in 1947 was predominately spotfin shiners, *Notropis spilopterus* (Cope), and southwestern sand shiners, *Notropis d. deliciosus* (Girard). The speckled dace, *Extrarius aestivalis* (Girard), apparently left the flooded areas with the recession of the river and did not occur in any of the samples taken in isolated backwater areas.

Spawning Periods of the Minnows

The minnows of the Des Moines River may conveniently be broken into three groups on the basis of spawning dates.[4] The early spawners are those that spawn in late spring or early summer. In this group the following species are included: central stoneroller, *Campostoma anomalum pullum* (Agassiz); western blacknose dace, *Rhinichthys atratulus meleagris* (Agassiz); hornyhead chub, *Nocomis biguttatus* (Kirtland); common emerald shiner, *Notropis atherinoides atherinoides* (Rafinesque); northern creek chub, *Semotilus a. atromaculatus* (Mitchill); brassy minnow, *Hybognathus hankinsoni* Hubbs; silver chub, *Hybopsis storerianus* (Kirtland); rosyface shiner, *Notropis rubellus* (Agassiz); and suckermouth minnow, *Phenacobius mirabilis* (Girard). Gravid females of the central stoneroller were taken in late May from the Des Moines River; however, very few young were observed. Too few specimens of the western blacknose dace and hornyhead chub were examined to determine their spawning dates in the river, but according to Hubbs and Cooper (1936), these species are early spawners. The spawning season of the common emerald shiner in the river is evidently early. A spent female was collected on July 17, 1946. Forbes and Richardson (1920) mention that *Notropis atherinoides* taken in Illinois from the middle of May to the first of June were greatly distended with eggs and were apparently about to spawn. Reighard (1910) in Michigan found that the creek chub spawned from the latter part of April to July. A few young chubs were taken from the Des Moines River in late July 1946. The spawning dates given by Reighard are probably applicable to the Des Moines since gravid females were taken in late April. Young northern common shiners, *Notropis cornutus frontalis* (Agassiz), were taken in late July of 1946 and 1947. The spawning of this species in the river seems to

[4] The spawning periods were determined by examination of the gonads, appearance of the young, and by reference to the literature. Turbidity of the water prevented direct observation of spawning activities.

occur from late June on up into the middle of July. According to Hankinson (1932) the common shiner in Michigan spawns from the latter part of May into June. The brassy minnow probably spawns in June, as evidenced by spent females. A few spent females of the silver chub were taken in the middle of June 1946. No young of this species was observed. A spent female of the rosyface shiner was taken on July 23, 1946. Prior to this date, all females examined had well developed eggs. Forbes and Richardson (1920) state that in Illinois females of *Notropis rubifrons* were ready to spawn in the latter part of May. The suckermouth minnow appeared to have spawned in late June and early July, 1946. No evidence of spawning was found in 1947 and 1948.

The bluntnose minnow, *Hyborhynchus notatus* (Rafinesque), and the fathead minnow, *Pimephales p. promelas* (Rafinesque), are placed in the group termed intermittent spawners, or fish capable of spawning throughout the warmer months of the year. The spawning of the bluntnose minnow in Michigan extends from the latter part of May to the latter part of August (Hubbs and Cooper 1936), at water temperatures of about 70° F. In the Des Moines River the successful spawning period of the bluntnose minnow appears to be confined to late July and August. At Fairport, Iowa, Markus (1934) found the spawning season of the fathead minnow to extend from May on into the middle of August. The spawning season was not definitely established for this species in the Des Moines River since too few specimens were obtained. Females taken in June and July of 1946 had well developed eggs.

The third group is the late spawners. These fish spawn from late July through August. In the Des Moines River this includes the spotfin shiner; southwestern sand shiner, central bigmouth shiner, *Notropis d. dorsalis* (Agassiz); bullhead minnow, *Ceratichthys perspicuus* (Girard); speckled dace; and river shiner, *Notropis blennius* (Girard).

Changes in Abundance of Various Species of Minnows

To determine the abundance of the various minnows, 619 collections were made from the Des Moines River with Common Sense minnow seines of 10, 20 and 30-foot lengths between April 9, 1946 and November 21, 1947. An additional 102 collections were omitted from the quantitative data because of either a fouled net or inclement weather conditions. In 1948 a few collections were taken in May, July and October.

The best measure of relative abundance is believed to be the percentage of the collections in which the species occurred (Table III). The average num-

Table III. *Percentage of occurrence of the more abundant species of minnows in the Des Moines River collections at various periods, 1946 to 1947*

Species	May 16 to Aug. 15, 1946	Aug. 15 to Dec. 14, 1946	March 28 to Aug. 15, 1947	Aug. 15 to Nov. 22, 1947
Notropis spilopterus	76	66	88	97
Notropis d. deliciosus	62	71	93	82
Notropis d. dorsalis	43	56	65	52
Extrarius aestivalis	10	57	73	70
Notropis cornutus frontalis	30	49	37	52
Hyborhynchus notatus	29	46	48	55
Ceratichthys perspicuus	8	31	73	58
Phenacobius mirabilis	10	32	21	27
Hybognathus hankinsoni	16	18	12	15
Pimephales p. promelas	15	10	18	24
Notropis rubellus	5	18	20	3
Semotilus a. atromaculatus	4	12	11	3
Number of collections	(254)	(199)	(108)	(33)

TABLE IV. *Average number per seine haul of the various species of minnows occurring in the Des Moines River collections*[1]

Species	May 16 to Aug. 15, 1946	Aug. 15 to Dec. 14, 1946	March 28 to Aug. 15, 1947	Aug. 15 to Nov. 22, 1947	Oct. 16–17, 1948
Notropis spilopterus	24.47	21.51	62.92	69.09	40.30
Notropis d. deliciosus	23.35	65.56	41.73	61.18	23.80
Notropis d. dorsalis	10.57	12.61	10.59	6.15	5.10
Extrarius aestivalis	0.66	6.90	19.57	27.94	2.60
Notropis cornutus frontalis	3.07	7.54	1.78	2.15	0.70
Hyborhynchus notatus	9.92	16.27	5.90	44.75[2]	19.70
Ceratichthys perspicuus	0.30	6.70	17.50	63.42[3]	7.50
Phenacobius mirabilis	0.37	2.58	1.07	0.48	0.50
Hybognathus hankinsoni	1.59	1.60	0.19	1.03	0.30
Pimephales p. promelas	1.01	0.42	0.33	0.91	0.00
Notropis rubellus	0.24	0.80	0.43	0.03	1.00
Semotilus a. atromaculatus	0.12	0.61	0.21	0.24	1.00
Campostoma a. pullum	0.34	0.42	0.19	0.03	0.30
Hybopsis storerianus	0.01	0.06	0.03	0.00	0.10
Notropis a. atherinoides	0.04	0.01	0.12	0.00	0.10
Notropis blennius	0.06	0.02	0.02	0.06	0.00
Nocomis biguttatus	0.00	0.00	0.06	0.09	0.00
Rhinichthys atratulus meleagris	0.01	0.01	0.00	0.00	0.00
Erimystax sp.	0.00	0.02	0.00	0.00	0.00
Number of seine hauls	254	199	108	33	10

[1] All samples corrected to 30-foot seine. 10-foot seine corrections were made by multiplying actual number of specimens by 3, and the correction factor for the 20-foot seine was 1.5.

[2] One seine haul accounted for 852 specimens representing 58 per cent of the specimens of *H. notatus* taken between August 15 and November 22, 1947.

[3] One seine haul accounted for 1,349 specimens representing 64 per cent of the specimens of *Ceratichthys perspicuus* taken between August 15 and November 22, 1947.

ber of individuals per collection (Table IV) also gives an indication of relative abundance but it is difficult to make comparable seine hauls at various times of the year.

The majority of the minnows collected were measured alive in the field and returned to the river. Age and year-class determinations of the minnows were made by using the length-frequency method (Lagler 1948), and by actually following the average size of a species as it appeared in the collections throughout the year. Length frequency distribution tables for a few of the more abundant species are given in the appendix. These tables represent a few selected samples taken at periods that indicate the changes in population. The fall of the year, particularly from the middle of October through November, was found to be an excellent period for collecting large samples of minnows in pools. These collections provided an adequate number of specimens to determine spawning success and the abundance of the various age-classes of a species. The speckled dace was an exception since it continued to inhabit the channel throughout the year, and it was therefore not taken abundantly in the pools as were the other common species.

The most abundant species of minnows in the Des Moines River are late spawners (Fig. 1). Apparently the usual high river stages in May and June limit the abundance of the early spawning species. The immediate direct effect of high river stages on spawning was not observed. The success of spawning was estimated from the occurrence of young in subsequent collections. The availability of food for young fishes is reduced by the increased turbidity, volume of water, and washing effect on bottom fauna and flora. The current possibly also washes downstream some eggs and fry of some species. The increase in erosion silt and siltation no doubt has a harmful effect on the eggs, fry, and food supply. Smith (1940), in

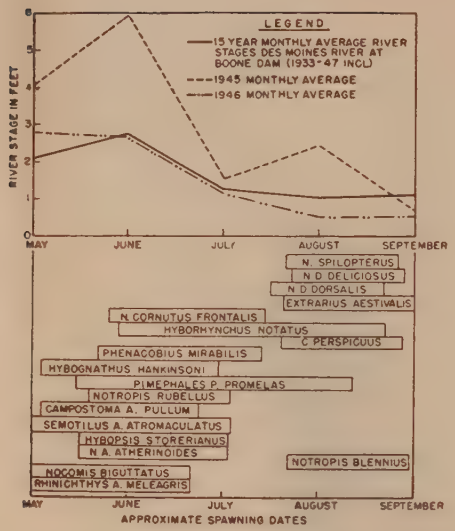

FIG. 1. Comparison of the approximate spawning dates of the Des Moines River minnows with monthly average river stages in Boone County, Iowa. The minnows are arranged in order of their abundance in the Des Moines River.

discussing silt in relation to salmon and trout, stated that silt may limit or entirely prevent successful reproduction of these fishes and probably limits the food supply. Neave (1948) mentioned the possible destructive effect more frequent and severe floods would have on the eggs and alevins of the pink and chum salmon in British Columbia. Langlois (1941) discussed the adverse effect the increased silt load has had on commercial fish production in Lake Erie. Ellis (1936) demonstrated experimentally that layers of silt from ¼ of an inch to an inch produced a very high mortality among freshwater mussels. The change of environment by increased volume as well as the elimination of possible suitable spawning sites perhaps postpones spawning for some species of fish. This could also result in absorption of eggs and a disinclination to spawn.

Bailey and Harrison (1948), in discussing the Des Moines River and other moderate-sized to large prairie rivers, state that they have some evidence to indicate that severe floods during the early and middle summer result either in poor reproduction or low survival of young fish. The present investigation of the mixed-species minnow population tends to substantiate this observation. The scarcity of young minnows subsequent to floods was noted in 1946 and 1947. However, during these years some species were quite successful as manifested by fall collections (Tables III and IV). These successful minnows were late and intermittent spawners. The time of floods is apparently an important factor controlling the species composition of the river minnow population, but an analysis of the changes in abundance of some of the species indicates that other factors may at times exert considerable effect.

The abundance of the speckled dace and the bullhead minnow varied more than any of the other species of minnows. During the spring of 1946 the speckled dace occurred in only 10 per cent of the collections, whereas a year later it occurred in 73 per cent of the collections. This increase in occurrence in 1947 was also quite apparent in the larger number of specimens occurring in each seine haul. In the fall of 1948 the speckled dace was scarce in the river and was taken only in 3 hauls, even though particular effort was made to collect this dace. The few specimens taken in the fall of 1948 were all adults.

The speckled dace is a short-lived, late-spawning fish and very few were found to attain an age over 1.5 years. The spawning of this fish is therefore largely dependent upon the one-year-olds. The low population early in 1946 was probably associated with the unusual floods during the normal spawning period in August 1945. The abundance of the 1946 year-class of the speckled dace in the fall of that year is indicative of the ability of this species to produce a large spawn from a low population comprised mainly of one-year-old fish. Water levels were apparently satisfactory for successful production of this species in 1946, 1947, and

1948, but only in 1946 was reproduction particularly successful. It is believed that population density and available space account for the failure in the two later years. In 1947 it was the speckled dace themselves that were abundant and in 1948 it appears that the abundance of other species may have been a limiting factor.

The change in the abundance of the speckled dace demonstrates the rapid fluctuation that an individual species can make within a mixed population. A change in the time of floods from spring and early summer to mid-summer could conceivably have a drastic effect on this species in the river. Several consecutive years of low-water levels prevailing through May, June and early July followed by high-water levels from mid-July through August would favor the early spawners and possibly the intermittent spawner, the bluntnose minnow. Such an environment would be unfavorable to the now abundant late-spawning minnows. Within a few years, a short-lived fish, like the speckled dace, would either be exterminated or reduced to an insignificant part of the population.

The changes in abundance of the bullhead minnow were similar to those of the speckled dace. There apparently was a spawning failure in 1945 and in the spring of 1946 only a few adult specimens were taken. The bullhead minnow spawned successfully in the summer of 1946 as did the speckled dace, and by fall of 1946 and spring of 1947 young of the bullhead minnow were very abundant in the river. The change in the frequency of the bullhead minnow from 8 per cent in the spring of 1946 to 73 per cent in the 1947 spring collections reflects the fluctuation of the abundance of this fish in the river. In the fall of 1948 the bullhead minnow again was found to be scarce in the river, its entire population being comprised largely of adults. This late spawner was found to attain an age of about five years; however, few over three years of age were taken from the Des Moines. The few specimens collected during the spring of 1946 were mostly two-year-old fish. The subsequent collections were comprised largely of fish of the year.

The spotfin shiner and the southwestern sand shiner were the two most abundant species in the river from the spring of 1946 through 1948, but the relative abundance between these two species changed. In the spring of 1946 the spotfin shiner occurred more frequently in the collections than did the southwestern sand shiner. By the following fall the southwestern sand shiner was more abundant than the spotfin shiner. This change in relative abundance came as a result of the successful spawning season of the southwestern sand shiner in the summer of 1946. In 1947 the spotfin shiner was the more successful spawner and in the 1947 fall collections occurred more abundantly than did the southwestern sand shiner. The collections taken in the spring of 1948 were largely composed of spotfin shiners. Spawning in 1948 was moderately successful for the spotfin shiner and virtually a complete failure for the southwestern sand shiner. In the fall of 1948 the southwestern sand shiner population was composed almost wholly of one- and two-year-old fish; whereas the spotfin shiner, having had some spawning success in 1948, was represented in the 1948 fall collections by young of the year as well as adults.

The southwestern sand shiner is a longer-lived fish than the speckled dace, occasionally reaching three years of age (Fig. 2). Early in 1946, the 1944 year-class was as abundant as the 1945 year-class, suggesting a partial failure of reproduction in 1945 due to the late summer high water. The two-year-old fish, which were abundant in 1946, were greatly reduced during the winter (1946–1947) and the early part of the following spring. It does not appear likely that predation was an important factor in causing this reduction since the only abundant predator, the southern channel catfish, *Ictalurus lacustris punctatus* (Rafinesque), feeds at a minimum in winter (Bailey and Harrison

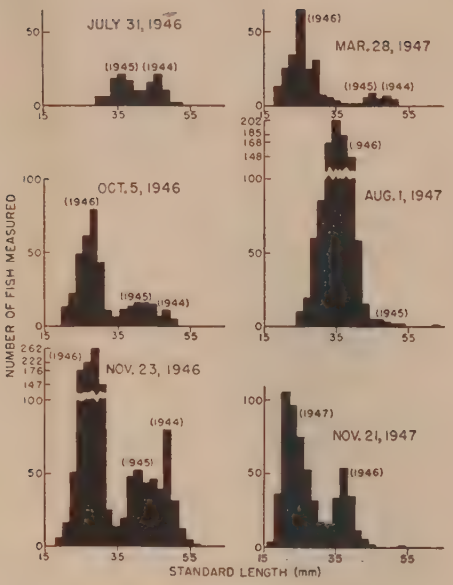

FIG. 2. Comparison of year classes of the Southwestern Sand Shiner (*Notropis d. deliciosus*) in the Des Moines River from six selected collections taken in 1946 and 1947.

1948). Several belted kingfishers, *Megaceryle alcyon alcyon,* were noted in the vicinity of the open channel at Station 2 throughout the winter. A few American mergansers, *Mergus merganser merganser,* were also observed on several occasions. The effect of these avian predators on the southwestern sand shiner was probably slight since this shiner for the most part remained under the ice cover along shore. At Station 3 where the entire river was covered with ice through the winter of 1946–47, a similar reduction in the two-year-old population was noted. Since no major changes in water level occurred during the winter there was no possibility of loss through stranding. Food was evidently not a factor as only 11 per cent of the 73 fish examined for food were empty. During this period no winter kills were noted or reported. The cause of the collapse of the two-year-old southwestern sand shiner population appears to have been senility.

The small 1945 year-class was also reduced during the winter of 1946–47. By August 1947, very few specimens of this year class appeared in the collections (Fig. 2). Most of the southwestern sand shiners collected in the summer and fall of 1947 were young of the year and one-year-old fish, in contrast to the 1946 collections which contained many two-year-old specimens. The scarcity of the two-year-olds (1945 year-class) may be traced back to the low reproduction of the southwestern sand shiner in August 1945. The spawning of the southwestern sand shiner was successful in 1946, moderate in 1947, and nearly a failure in 1948. Low water prevailed in mid-July through August all three of these years. The poorer production in 1947 and 1948 was probably associated with the higher population density and lower amount of available space as has been postulated for the similar trends in the speckled dace population.

Another factor should perhaps be mentioned in connection with the changes in the population of southwestern sand shiners. In 1947 the spawners were largely one-year-olds, whereas in 1946 and 1948 many of the shiners were two years old. Egg counts on several specimens for each age group of the southwestern sand shiner were made using the method described by Ulrey, Risk, and Scott (1938). It was found that one-year-old females in late July contained about 250 eggs, two-year-olds 1,100, and three-year-olds 1,800 eggs. Spent one-year-old females were taken in August, 1946 and 1947, indicating that they do spawn. The one-year-old fish in 1947 were approximately as abundant as the one- and two-year-old fish combined in 1946. The lower reproduction in 1947 might be partially attributed to the scarcity of the more fecund two-year-old fish. Three-year-olds were scarce throughout the entire investigation. Age-class composition might also modify the seriousness of reproductive failure in different years. The effect of high water in August during the spawning season of the southwestern sand shiner in the presence of a dominant one-year-age class such as probably was

the case in 1945, as indicated by the abundance of two-year-old fish in subsequent collections, was possibly of less importance on the population than if it had been a year with a dominant two-year-age class. An unsuccessful spawning in 1946 would have had a drastic effect on this species; whereas, in 1947 high water in August or some other unfavorable condition would have had less effect, provided spawning conditions had been favorable in 1948.

The spotfin shiner is a longer-lived late-spawning species than either the speckled dace or the sand shiner and its population changes show many of the same features as have already been discussed for these species. The 1945 year-class of the spotfin shiner was not abundant in 1946 and was probably affected by the high water in August 1945. In 1946 the 1944 year-class appeared nearly as abundant as the 1945 class. The spotfin shiner lives to be five years of age or more in the river and the first three classes appeared regularly in the collections. In 1946, a group determined as five-year-old fish (1941 year-class) was occasionally taken, whereas in 1947 only one five-year-old (1942 year-class) occurred in the collections. A review of the river stage data for 1941 and 1942 reveals that the river was very low in late July and August in 1941 as compared to 1942. This possibly further illustrates the effect of water levels and turbidity on the abundance of year-classes of the spotfin shiner in the river. Space apparently does not affect the spawning of the spotfin shiner as much as it does that of the speckled dace and southwestern sand shiner. With the limited space and high populations in 1948, the spotfin shiner was the only minnow that showed any success in spawning.

The late-spawning central bigmouth shiner had a somewhat similar history to that described for the southwestern sand shiner. Two-year-old central bigmouth shiners were abundant in the river in 1946 and quite scarce in 1947, similar to the findings on the southwestern sand shiner. The central bigmouth shiner did not have as successful spawning seasons in 1946 and 1947 as it evidently did in 1944. Some evidence of a dominant year-class of this species was also noted in several of the small tributary streams surveyed. This species was the only minnow that was abundant both in small streams and in the Des Moines River. The fact that this species showed less pronounced changes in abundance than some of the others may indicate that some of the bigmouth shiners may move from the small streams into the river at various times.

The river shiner was the only late spawning minnow which was present in the river but not taken in numbers during the 1946–48 period. Apparently it was quite abundant in 1940 (Starrett 1950a).

The intermittent spawners might be expected to have an advantage over all other species since they could spawn whenever water levels were proper. On the other hand their spawning would not be as intensive and therefore perhaps not as successful when space became a factor. The bluntnose minnow was fairly abundant throughout the period of study. In 1946 and 1947 it did not spawn successfully until late July and early August, due to the high water stages earlier in the year. In 1948 an early appearance would have been expected for the young of bluntnose minnow, but the species was not very successful in spawning at any time during that year. The bluntnose minnow was abundant in the river in the spring of 1948, and it is believed that spawning failure was associated with limited space because of low-water conditions and that the population was not reduced by isolation following high-water levels as in previous years.

The fathead minnow is also an intermittent spawner but was not abundant in the Des Moines. The possibility that the fathead minnow is limited in its distribution in Boone County because of its intolerance to other species is mentioned elsewhere (Starrett 1950a).

Most of the early spawners were taken too infrequently in the Des Moines River to study their population changes. The northern creek chub was the most abundant species and the observations suggest how this species maintains itself even though spawning conditions are seldom suitable. The creek chub occurred more abundantly in the small tributary streams in Boone County (Starrett 1950a) where the run-off was rapid and the water level tended to stabilize much faster than in the river. In 1946 and 1947 this species spawned successfully in the small tributary streams. Chubs taken during this period in the river were chiefly sub-adults and adults. It appears then that the sub-adults occurring in the river were of small-stream origin and that the river population of this chub may be partially or wholly dependent upon this source for replenishment in unfavorable years. In 1948, a year of continued low-water levels, a few young chubs were taken from the river. The tributary streams were not checked in 1948.

The high-river stages appear to be important in controlling the abundance of several species of minnows. Since in most years the high stages come in May and June, the late spawning species are favored and are the most abundant species in the river. The amount of space available during the lower water stages and the extent to which this space is occupied by minnows, and perhaps by other species as well, appear to control to a considerable extent the success of reproduction each year. It seems that floods may have a beneficial effect on the minnow population by thinning the population and providing space for young fish. In the springs of 1947 and 1948 the minnow populations were high, particularly the spotfin shiner and southwestern sand shiner. In both years the water was low in late summer. However, as has been mentioned, the 1947 population was subjected to flood in June and early July and many of the minnows were stranded in isolated pools outside the river, whereas the 1948 population was not. It is believed by the writer that the spawning failures of the minnows in 1948 were associated with high populations that were not reduced by floods as in previous years. Limited amount of space coupled with a high population proved unsatisfactory for successful spawning. With short-lived species like most of the minnows it might be beneficial if the population were thinned each year so that there would be successful reproduction whenever water levels were suitable. If a population is high early in the spawning season and because of lack of space is rather unsuccessful in reproduction, most of the minnows the next season will be reaching the end of their normal span of life and a failure in spawning because of high water may be quite serious.

Discussion of Similar Phenomena in Other River Fishes

The river carpsuckers (*Carpiodes* spp.) are as a group very successful in the Des Moines River. Fry of these fishes occurred abundantly in July 1946; however, very few were taken in 1947 and 1948. The water levels remained high up into the middle of July in 1947 in contrast to low-water levels in July, 1946. No explanation other than lack of space is given for its spawning failure in 1948.

The southern channel catfish is the most abundant game fish in the Des Moines River. This species spawns in the Des Moines in July (Harrison 1947). The ability of the catfish to spawn after June, when water levels are usually more stable and less silt load is carried by the river, appears as an important factor in the abundance of this fish.

Although carp, *Cyprinus carpio* Linnaeus, are not late spawners, they occur abundantly in the Des Moines River. Carp of the year seldom appeared in the river itself. At Station 2 (Fraser, Iowa) a small borrow pit is adjacent to the river. This pit is connected with the river only during periods of high water. Seining here revealed the presence of both

young and adult carp. It appears that the Des Moines carp population could be supported largely from such pits and ponds near the river. A flood following a successful spawning season would permit access to the river for the young and adults. No attempt was made to correlate water levels and dominant age-classes of carp.

In Iowa the northern smallmouth black bass, *Micropterus dolomieu dolomieu* Lacépède, spawns in May and June. Through the years 1946 and 1947 only one young smallmouth bass appeared in the river collections. In 1947 spawning of this species was successful in two small tributary streams of the Des Moines in Boone County. These streams have small watersheds. The stream gradient is higher than that of the river, giving faster run-offs and less silting. In July 1948, a year without floods, K. D. Carlander and R. Fredin took 12 young smallmouth bass in a minnow seine at Station 2. Fall collections in 1948 also revealed the presence of young bass. The spawning success of the smallmouth bass in the Des Moines appears correlated with water levels. Other factors such as population size, available food and water temperatures were apparently favorable in the river in 1946 and 1947. However, floods occurred during the spawning seasons of those years. Johnson (1949, p. 38) found a similar trend relative to floods and spawning success of the smallmouth bass in Minnesota. "Streams near Mankato and New Ulm once were good producers of smallmouth bass but ten consecutive years of spring floods and silty freshets have stopped most spawning attempts and the bass population is now at low ebb." Dr. Johnson (letter, December 21, 1948) states regarding these two streams that: "In 1948 when there was not a single flood, we found about 35 small bass per acre which had just been hatched during May. The few breeders remaining had been able to spawn successfully for the first time in a decade."

In the same letter, Dr. Johnson mentions that in 52 trout streams in southwestern Minnesota natural reproduction of trout is almost non-existent except in five streams. These five streams have very small watersheds and rarely flood. Quoting Dr. Johnson's letter: "In 1948, there were no floods in any of the 52 streams, and for the first time in 26 years, small trout have appeared in nearly all of those waters. They were not hatchery trout."

The combination of floods and heavy silt loads appears to be an important limiting factor not only to minnows but other species of fishes as well. The importance of space has been stressed here for the minnows and it should be considered as a possible important factor for other river fishes. Continued low-water levels would reduce space and successful spawning of many fish. The reduction of minnow populations through isolation following a high water period appeared to have a beneficial effect on subsequent spawning of two species of minnows. Such a reduction may similarly affect other fishes.

Summary

Fish collections were made in the Des Moines River, Boone County, Iowa, from 1946 through 1948. Emphasis in the investigation was placed on the changing abundance of the various species of minnows. The spotfin shiner and southwestern sand shiner were consistently the most abundant minnows in the river.

Floods and silt appear to be important factors affecting the Des Moines River fish population. The abundant species of minnows in the Des Moines spawn in late July and August, a period usually with low-water levels and reduced silt loads.

Population size and space are considered to be important factors in limiting spawning success of minnows. Spawning failures of minnows occurred when water levels remained low throughout the year and when the population size was high. Isolation of abundant minnows in temporary backwaters following a flood re-

duces that population and it appears that this might be beneficial to the population.

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APPENDIX TABLE I. *Length-frequency distributions of the spotfin shiner,* Notropis spilopterus, *Des Moines River*

Standard length in millimeters	June 27–July 10, 1946	Sept. 17–28, 1946	May 30, 1947	Aug. 9–10, 1947	Nov. 21, 1947	Oct. 16–17, 1948
14–15	—	2	24	—	7	—
16–17	—	2	29	—	42	5
18–19	—	5	41	—	272	15
20–21	—	14	96	1	209	10
22–23	—	24	162	15	98	22
24–25	—	30	110	71	58	33
26–27	12	12	71	119	37	38
28–29	24	18	35	104	35	35
30–31	13	12	13	41	34	15
32–33	18	12	5	23	70	27
34–35	18	3	11	19	45	16
36–37	27	5	2	22	25	29
38–39	14	3	3	24	30	28
40–41	2	5	1	13	5	12
42–43	7	7	1	20	3	25
44–45	9	4	—	17	1	19
46–47	6	5	—	19	—	13
48–49	6	10	2	10	1	14
50–51	9	10	1	1	—	8
52–53	9	5	1	6	—	8
54–55	4	6	—	7	—	7
56–57	3	1	1	1	—	5
58–59	3	1	2	1	—	4
60–61	2	1	—	—	—	4
62–63	1	—	—	—	—	3
64–65	1	—	1	—	—	1
66–67	1	—	1	—	—	—
68–69	2	—	1	—	—	—
70–71	1	—	—	—	—	—
72–73	1	—	—	—	—	—
74–75	2	—	—	—	—	—
Total number	195	197	614	534	972	396

APPENDIX TABLE II. *Length-frequency distributions of the southwestern sand shiner,* Notropis d. deliciosus, *Des Moines River*

Standard length in millimeters	July 31, 1946	Oct. 5, 1946	Nov. 23, 1946	Mar. 28, 1947	Aug. 1, 1947	Nov. 21, 1947	Oct. 16–17, 1948
16–17	—	2	1			3	1
18–19	—	2	5	14		37	3
20–21	—	13	17	26		105	3
22–23	—	25	50	34	1	96	1
24–25	—	49	176	65	10	75	1
26–27	—	63	222	24	19	53	3
28–29	—	79	262	31	60	32	3
30–31	6	43	147	7	86	17	14
32–33	6	12	25	6	168	16	18
34–35	18	6	13	4	202	33	26
36–37	21	11	19	1	185	54	37
38–39	17	13	47	2	148	35	36
40–41	9	16	52	2	58	11	36
42–43	9	16	43	5	16	5	26
44–45	16	15	46	9	5	1	20
46–47	21	6	39	5	5	—	7
48–49	9	11	79	7	4	—	—
50–51	1	5	31	4	2	1	1
52–53	1	—	12	1	2	—	—
54–55	—	1	3	1	—	—	—
56–57	—	—	1	—	—	—	—
58–59	—	—	—	—	—	—	—
60–61	—	—	—	—	—	—	—
62–63	—	—	—	—	1	—	—
Total number	134	388	1,290	248	972	574	236

APPENDIX TABLE III. *Length-frequency distributions of the central big-mouth shiner,* Notropis d. dorsalis, *Des Moines River*

Standard length in millimeters	Aug. 1, 1946	Nov. 22–23, 1946	Mar. 28, 1947	May 16, 1947	Oct. 12, 1947	Oct. 16–17, 1948
18–19	—	—	1	—	—	—
20–21	—	—	5	—	—	—
22–23	—	2	11	3	2	2
24–25	—	3	12	6	—	—
26–27	—	13	9	17	1	—
28–29	1	16	19	20	—	—
30–31	—	57	24	26	—	2
32–33	2	45	9	20	—	1
34–35	3	49	11	16	—	1
36–37	5	18	5	7	3	1
38–39	7	10	12	5	2	2
40–41	7	4	10	7	2	4
42–43	3	6	19	20	13	8
44–45	3	3	14	13	7	4
46–47	1	2	9	18	9	8
48–49	—	2	7	9	5	6
50–51	1	1	10	5	1	2
52–53	—	1	1	4	—	4
54–55	—	—	2	1	—	6
56–57	—	—	2	—	—	1
58–59	—	—	2	—	—	—
60–61	—	—	1	—	—	—
Total number	33	232	195	197	45	52

APPENDIX TABLE IV. *Length-frequency distributions of the speckled dace,* Extrarius aestivalis, *Des Moines River*

Standard length in millimeters	July, 1946	Oct. 29, 1946	May 16, 1947	July 17, 1947	Oct. 18, 1947	Oct. 16–17, 1948
18–19	—	—	2	—	1	—
20–21	—	1	—	—	—	—
22–23	—	11	—	—	12	—
24–25	—	39	5	1	60	—
26–27	—	33	11	4	79	—
28–29	—	30	28	6	23	—
30–31	1	7	45	14	7	—
32–33	1	2	48	42	3	—
34–35	6	2	54	79	14	1
36–37	3	2	18	60	14	—
38–39	1	5	11	40	38	—
40–41	—	3	5	25	24	5
42–43	—	—	6	7	11	7
44–45	—	1	4	3	15	2
46–47	1	—	1	1	1	6
48–49	—	—	—	1	1	5
50–51	—	1	1	—	—	—
52–53	—	—	1	—	—	—
Total number	13	137	240	283	303	26

APPENDIX TABLE V. *Length-frequency distributions of bullhead minnow,* Ceratichthys perspicuus, *Des Moines River*

Standard length in millimeters	June, 1946	April 13, 1947	Aug. 16, 1947	Nov. 21, 1947	Oct. 16–17, 1948
12–13	—	—	1	—	—
14–15	—	—	1	—	—
16–17	—	4	2	9	—
18–19	—	35	—	64	—
20–21	—	68	—	314	—
22–23	—	96	—	470	—
24–25	—	98	—	334	—
26–27	—	51	8	158	—
28–29	—	38	23	63	—
30–31	—	26	11	31	—
32–33	—	11	10	32	—
34–35	1	14	9	26	1
36–37	—	8	4	17	—
38–39	—	7	1	10	—
40–41	3	6	3	9	3
42–43	—	3	—	8	—
44–45	4	—	1	4	4
46–47	3	—	1	3	3
48–49	2	—	1	3	2
50–51	1	—	1	—	1
52–53	—	—	—	—	—
54–55	3	—	1	4	3
56–57	2	—	—	1	2
58–59	4	—	—	1	4
60–61	—	—	—	—	—
62–63	—	1	—	—	—
64–65	—	—	—	—	—
66–67	—	1	—	—	—
68–69	2	—	—	—	2
Total number	25	467	78	1,561	25

APPENDIX TABLE VI. *Length-frequency distributions of the bluntnose minnow,* Hyborhynchus notatus, *Des Moines River*

Standard length in millimeters	July, 1946	Nov. 23, 1946	Aug. 23, 1947	Nov. 21, 1947	Oct. 16–17, 1948
18–19	—	—	—	4	1
20–21	2	2	1	42	—
22–23	—	7	1	184	2
24–25	—	23	—	242	1
26–27	1	62	—	218	1
28–29	1	75	—	114	2
30–31	3	105	—	38	—
32–33	2	125	4	9	2
34–35	5	76	7	5	8
36–37	3	44	30	30	20
38–39	9	30	25	60	33
40–41	3	13	19	44	30
42–43	4	3	29	41	25
44–45	6	6	5	16	18
46–47	3	11	9	5	14
48–49	3	9	8	7	10
50–51	4	6	8	6	6
52–53	1	5	10	12	2
54–55	—	1	8	7	3
56–57	—	—	2	1	1
58–59	—	4	2	—	3
60–61	—	3	1	—	3
62–63	—	2	—	1	2
64–65	2	1	—	—	3
66–67	—	—	—	—	—
68–69	1	—	—	—	—
Total number	53	613	169	1,086	190

CAMBIAL FROST INJURIES AND MULTIPLE GROWTH LAYERS AT LUBBOCK, TEXAS

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Among the many workers who have investigated the effects of frost on plants, some were primarily concerned with internal effects (Caspary 1857, Hartig 1895, Rhoads 1923, Hemenway 1926, Harris 1934, Day and Peace 1934 and 1937, Stone 1940) whereas others were concerned more with external effects (Busse 1910, Deters 1938, Chandler 1945). The extent of the interest is well shown by the bibliography of Harvey (1936).

A previous communication (Glock and Reed 1940) set forth that heavy frosts are of common occurrence after tree growth has begun in the spring at Lubbock, Texas, that such frosts may be of sufficient intensity to distort or crush newly formed cambial derivatives in branches and leaders, that the frost injuries mark the inner parts of annual growth increments, and that certain years were thus marked.

The present purpose is to add some necessary details to the previous work, to describe the evidence by which specific dates were assigned to the frost injuries, to supply illustrations, and to trace the effects of the 1938 frost in later years.

MICROSCOPIC FROST INJURY

Details of the year 1938 will be used as an example. The campus of Texas Technological College at Lubbock, where the observations to be described were made, lies at an elevation of 3,200 feet on the southern part of the High Plains and, with an annual rainfall of slightly more than 19 inches, the area is equivalent ecologically to the extreme lower forest border. No trees grow here naturally; all the observations were made on trees that had been introduced.

In December, 1938, stained transverse sections were made from branches of Arizona cypress (*Cupressus arizonica*) growing on the college campus. Among the stained sections an intense frost injury was immediately recognized near the inner margin of the outermost growth layer.

Recognition of frost injury has been greatly facilitated by the work of Bailey,[3] who described (1925: 94) the results of frost injury in the following words: ". . . the rings of distorted tissue consist in part of crumpled tracheids and in part of crushed, undifferentiated, centripetal derivatives of the cambium." Rays are commonly offset at the line of injury. Experiments carried on with the collaboration of Dr. R. A. Studhalter (Studhalter and Glock 1942) have shown that in the case of a severe frost portions of the cambium may be killed outright and thus require regeneration before growth can continue. At the start of recovery the newly derived cells tend to be enlarged and deformed. As recovery proceeds successive cells gradually assume normal size and form.

The frost injury near the inner margin of the outermost growth layer was "dated" as having occurred early in the 1938 growing season on the evidence of phenological observations, temperature records, and radial position in the xylem.

Phenological observations recorded "killing frosts" during the nights of April 7–9, 1938.

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[2] To Dr. A. Wetmore and the Smithsonian Institution the writer is deeply indebted for grants of financial aid. He is grateful to Dr. Charles J. Turck and Macalester College for the time and facilities to carry on tree-ring studies.

[3] The writer is grateful for the pleasant and instructive hours he spent at a microscope with Dr. I. W. Bailey who so clearly taught the anatomy of frost rings and cell structure.

Frost days [4] are not uncommon at Lubbock, Texas. An interval of several consecutive frost days is much less common and an ice day is comparatively rare. A tabulation of the maximum and minimum Fahrenheit temperatures for pertinent intervals with included frost days during March, April, and May, 1938, is shown in the table in the next column. The wind velocity on April 7 was recorded as 20 miles per hour, on April 8 as about 15 miles, and on April 9 as about 5 miles. The maximum temperature of 35° on April 8 was the closest to an ice day of the entire winter except for February 7 with 35° and the previous

[4] A frost day according to Landsberg (1947: 118) is one whose minimum temperature is below freezing, and an ice day is one whose maximum is below freezing.

		Max.	Min.
March	6	59	26
	7	63	30
	19	76	30
	20	83	41
	21	83	50
	22	77	45
	23	69	30
	31	65	31
April	1	48	36
	2	59	25
	3	75	34
	4	85	37
	5	85	50
	6	73	41
	7	41	24
	8	35	23
	9	67	28
	10	72	41
	11	74	50
May	8	72	32

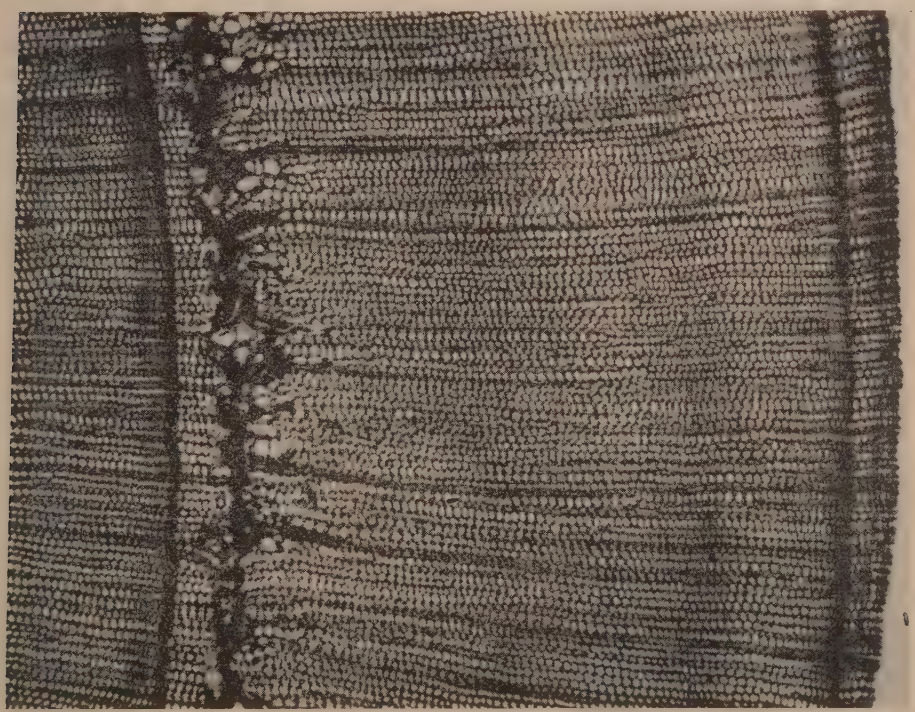

FIG. 1. Arizona cypress. Transverse section showing outer part of 1937 annual increment (left) and entire 1938 with its three growth layers (right). Frost injury of April 7–9, 1938, and recovery, lie near inner margin of 1938 (left). Section taken December, 1938. Scale: about × 55. Photo by Harold M. Hefley.

December 9 with 32°. On the whole, the interval, April 7–9, which experienced the lowest temperatures of the three months, March, April, and May, was the logical one to have produced a frost injury.

Cambial activity, of course, must have begun prior to the impact of frost in order that the newly formed cambial derivatives could be affected. During March, 1938, 22 days had maximum temperatures of 70° or above, and of these, six were above 80°. Such conditions no doubt brought about the initiation of growth sufficiently early in the season to permit the formation, on the average, of four to six xylem cells before the frost injury occurred.

Therefore, the combination of phenological observations, temperature records, and position of the frost injury at the time of sampling gave rather conclusive evidence that the tissue injury near the beginning of the outer growth layer in the stained sections was caused by the severe frosts of April 7–9, 1938.

During the winter of 1938–1939, immediately following the discovery of the spring 1938 frost injury in the trees on the campus of Texas Technological College, many stained sections were made from different trees, from different branches of the same tree, from different distances back of the branch tip on the same branch, and from the leaders of two trees. The injury has by now been found in 16 different species; these include, *Cupressus arizonica, Fraxinus* sp., *Gleditsia triacanthus, Hibiscus syriacus, Junip-*

Fig. 2. Arizona cypress. Transverse section of stem showing, from left to right: outer part of 1934 annual increment with its multiple dense wood, the five growth layers of 1935 annual increment, and the inner part of 1936 with its zone of frost injury and recovery. Scale: about × 50. Photo by Harold M. Hefley.

erus virginiana, Pinus jeffreyi, P. ponderosa, P. ponderosa?, P. sp., *P. taeda, Platanus occidentalis, Populus* sp., *Pyrus malus, Thuja* sp., *Ulmus parvifolia,* and *Vitex agnus-castus.* A large share of the materials studied, however, came from Arizona cypress and yellow pine (*Pinus ponderosa?*). No frost injury of the cambium has yet been found in *Acer saccharinum* and a few other species.

Many of the sections made during the winter showed a common but surprising phenomenon: the insertion of extra growth layers between the cambium and the growth layer containing the 1938 frost injury. This was particularly striking in sections taken at intervals along a single branch. In a majority of cases the extra growth layers were so sharply bordered that they could not be distinguished from true annuals. Because of these observations it was realized, in February, 1939, that the 1938 frost injury marked off the true radial extent of the xylem formed during 1938 whether or not it contained one or more growth layers. The frost gave a means of exact dating through the fact that it had "tagged" the growth layer formed at that time.

Figure 1 is an example from a branch of an Arizona cypress showing, first, the 1938 frost injury and recovery beginning some six cells out in the 1938 growth and, second, two distinct growth layers in the annual increment. In addition, the figure

FIG. 3. Ponderosa (?) pine. Transverse section of stem. From left to right between the arrow tips are seen: frost injury of 1936, and six dense wood layers of 1936–1937 (the "x" marks the division between 1936 and 1937 growth), and immediately to the right of the right arrow point, the frost injury of April 7–9, 1938. Scale: about × 35. Photo by Harold M. Hefley.

shows a portion of a diffuse lens as the outermost part of the increment.

With the frost injury of April 7–9, 1938 as a guide, the method was extended backward to the growth for 1932. Diagnostic injuries were found in 1932, 1933, 1934, 1936, and slight injury in 1937. Reference to Weather Bureau records showed that the injuries of 1936 and 1937 must have occurred on April 2, 5–8, and March 26–31, respectively. No injury existed in the increment for 1935 and none could be expected because temperatures at no time fell below freezing after the night of March 8. An example of the use of these injuries for dating purposes is given in the section of figure 2 which came from the stem of an Arizona cypress. The section shows, from the inside outward: first, the outer part of the 1934 increment with a diffuse margined growth layer and multiple dense wood; second, five sharp growth layers in 1935; and third, the inner part of 1936 with its frost injury typically very close to or at the inner margin of the increment. In some cases, the multiplicity of 1935 is either not so well defined as here or else several of the growth layers are lenticular tangentially and longitudinally. Nevertheless, the tendency toward multiplicity in 1935 characterizes the trees of the Lubbock area.

A final example of the use of frost injury in dating is shown in the ponderosa(?) pine sections of figures 3 and

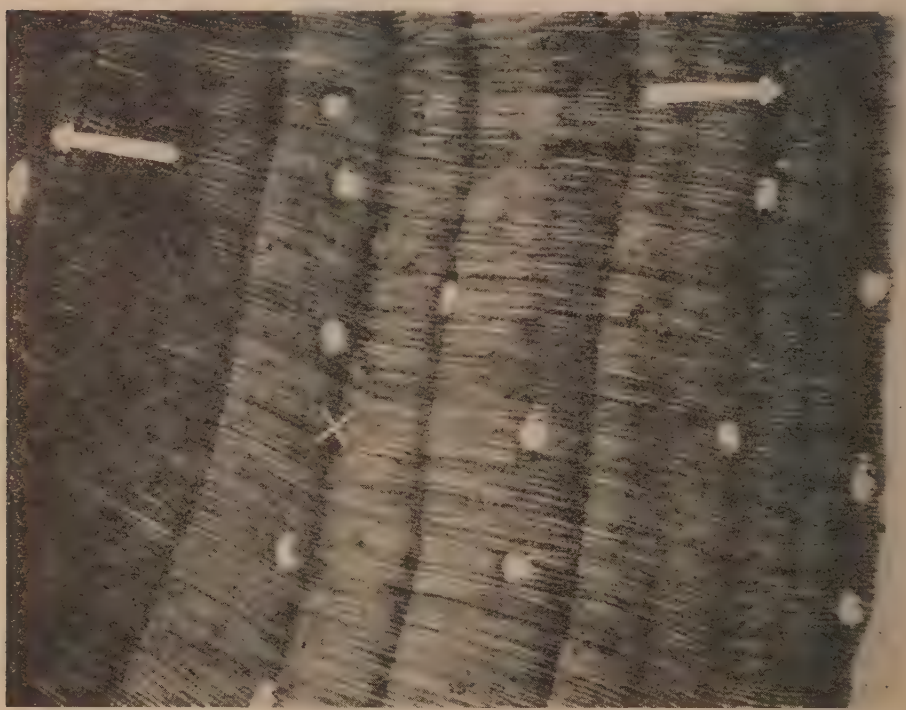

FIG. 4. Another section from the Ponderosa (?) pine of figure 3, and showing the same time interval. Here, frost injury of 1937, lies in the ring immediately to the right of the "x," which separates 1936 annual increment of two layers from 1937 increment of three layers. It will be noted that there is no comparable frost injury in the ring to the right of the "x" in figure 3. Scale: about × 40. Photo by Harold M. Hefley.

4 which are portions of two branches of the same tree. The frost injury outward (toward the bark) from the right arrow point, figure 3, is that of 1938 whereas the injury outward from the point of the left arrow point is that of 1936. Therefore, the arrows span the growth layers formed during the 1936–1937 growing seasons. Where is the boundary between the two seasons? The arrows in figure 4 span the same five growth layers as in figure 3. But there is a feature added to figure 4: it contains the frost injury of 1937 located just to the right of the "X." Hence, the 1936 annual increment contains two growth layers and that of 1937 contains three.

Macroscopic Frost Injury

The injury of 1938 was the most intense and the most universal of all frost injuries examined and dated under the microscope. However, the effects were not confined exclusively to that year. They were prolonged into the following years because the xylem had been so severely ruptured that the branches, and even the trunks, were seriously weakened.

Fig. 5. Chinese elm. Transverse section, saw-cut surface, showing dark band of April 7–9, 1938, frost injury at end of pointer. Section taken April, 1940. Scale: × 2½. Photo by H. W. Gross.

In the early spring of 1940, the mortality rate among the Chinese elms of the Lubbock area became surprisingly high either by outright death, or by death of portions of the crown, or by mechanical breakage. An examination of dozens of branches of diameters large enough to have experienced the frost of April 1938, and many trunks which had broken or died, consistently showed even in rough-sawed sections, a dark band (fig. 5) near the inside of the second main growth layer in from the bark. When the wood section of figure 5 was polished (fig. 6) it showed the dark band to be an injury which had more or less completely ruptured the woody tissue. The open tangential crack in figure 7 illustrates an extreme case of frost injury. Figures 6 and 7 are typical examples of the mechanical injury which so weakened the affected branches that they could not withstand the winds of early spring.

The 1938 frost injury not only prevailed throughout the branches examined but also extended in some cases down into basal trunks several of which were up to eight inches D.B.H. In fact,

FIG. 6. Chinese elm. Polished end of figure 5 section. Frost injury of April 7–9, 1938, shows as a circular crack at the end of the pointer. Radial position of the injury shows differing amounts of xylem formed around circuit before freezing occurred. Scale: × 2½. Photo by H. W. Gross.

one tree cut down in April, 1942, showed a tangential crack in the early part of the 1938 growth layer a foot above the ground where the trunk (April, 1942) was 10 inches in diameter.

Another interesting sequel to the frost of 1938 came to light on April 6, 1948, when a deodar cedar (*Cedrus deodara*) was felled on the campus of Texas Technological College. Figure 8 shows a section from the basal trunk. The frost injury of 1938 appears at the end of the pointer as a dark line separating the inner lighter-toned heart wood from an outer dense-brown heart wood. A hand-lens (× 14) brings out the injury in an unmistakable manner. In addition, the main body of the third growth layer inward from the 1938 injury, presumably the increment for 1935, contains multiple bands of dense wood, a multiplicity already noted in figure 2.

The section of cedar emphasizes the value of the 1938 frost injury as an instrument of dating because 14 sharply defined growth layers and one lens occupy the interval, 1938–1947. Figures 1 to 4 with more than one growth layer per year add to the emphasis. As a matter of fact, this situation of multiple growth layers caused by multiple waves of cambial activity during one season of growth characterizes the lower forest border where it has been investigated.

FIG. 7. Chinese elm. Transverse section showing at end of pointer, a crack developed as an arc in the light wood by the April 7–9, 1938, frost injury. Section taken April, 1940. Scale: × 1½. Photo by H. W. Gross.

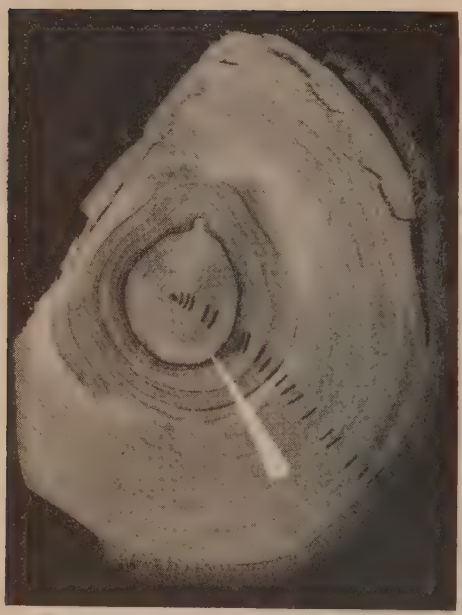

FIG. 8. Deodar cedar. Transverse section of basal stem showing April 7–9, 1938, frost injury at end of pointer. Short black lines separate sharply margined growth layers. Section taken April 6, 1948. Scale: × ⅞. Photo by H. W. Gross.

SUMMARY AND CONCLUSION

It is clear, as Bailey (1925) has pointed out, that frost injuries can be used as "indicators of the chronology of specific biological events." Also, it is clear that frost injury and recovery can be used to assign exact dates to growth layers and thereby delineate annual additions to the xylem no matter how multiple they may be. The time when growth begins and the characteristics of the temperature régime make the Lubbock area well adapted to a study of natural frost and its effects on the 16 kinds of trees examined. All of these species had been artificially introduced into this naturally treeless High Plains region.

There remains the task of tracing accurately dated annual increments from the branches down into the basal trunk in order to determine whether or not growth-layer habits, such as multiplicity and lenticularity, extend throughout the tree. A portion of this work has been done. A study of the environmental causes of multiple growth-layer formation in a single year is also being carried on.

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FURTHER ECOLOGICAL STUDIES ON STRATIFICATION OF THE ARTHROPODA [1]

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Introduction

This study is a comparison of stratification of arthropods in an oak-hickory association with that in red cedar consocies.

Since 1921 several quantitative community studies have been made with varying degrees of emphasis on stratification. Among these studies are those by Sanders and Shelford (1922), Weese (1924), Blake (1926), Davidson (1930), Brown (1931), Fichter (1939), Jones (1946), and Dirks-Edmunds (1947). Other authors have commented as follows:

"Some animals are commonly found on the ground, others on the herbs and still other species at different levels in the shrubs and trees. This is termed stratification" (Adams 1941).

"Each layer of vegetation has an environment quite different from that of the other" (Weaver and Clements 1929).

Shelford (1937) notes that "the migration of animals from one stratum to another makes the division lines difficult to draw in some cases. Still, the recognition of strata is essential but rigid classification undesirable." He maintains that "strata are groups of consocies occupying the recognizable vertical division of a uniform area."

The author wishes to acknowledge his indebtedness and express his sincere thanks and appreciation to the following specialists in the taxonomic determination of material belonging to special groups: C. C. Hoff, Pseudoscorpionida; Willis J. Gertsch, Araneida; R. A. Hefner, Myriapoda; A. B. Gurney, Orthoptera and Corrodentia; R. I. Sialer, Hemiptera; P. W. Oman, Homoptera; C. A. Frost, Coleoptera; C. Heinrich, Lepidoptera; C. W. Sobrosky, W. W. Wirth, Alan Stone, Diptera; Mary Talbot, Formicidae; C. F. W. Muesebeck, L. J. Weld, B. D. Burks, K. V. Krowbein, A. B. Gahan, all other Hymenoptera. Some of the more common species were determined by the author. Thanks are also due my colleague T. D. Pawley of the Department of English for reading and correcting the manuscript, and to W. C. Van Deventer of Stephens College for reading and criticizing a part of the manuscript.

Locality and Methods

The area studied comprises about 200 acres and is located adjacent to and west of Highway 54, twelve miles south of Jefferson City, Missouri. It is a part of the Otto Neihorn tract. It is a climax oak-hickory association with about five acres of red cedars in the developmental stage located near its eastern border. One collecting station was established in each of the above communities. The collecting grounds in both communities are higher than the surrounding area. The angle of incline is about 35 per cent. Drainage is in the main toward the north and ultimately into the Missouri River which is about 13 miles distant. Mr. Neihorn, who inherited the place from his ancestors, is quite positive that no fires have occurred in the woods during the past 65 years. The entire area is fenced in and used as a pasture for cattle, but there is very little evidence that the collecting areas had been used or trampled over by the cattle. Perhaps most of the grazing is done in the lower open areas where the soil is richer and consequently the grasses are much better for feeding. Few of the trees have been cut down. The area would thus be considered a secondary one.

[1] This work was accomplished with the support of a grant from the Penrose Fund of the American Philosophical Society for which the author is very grateful.

The rock is the Jefferson City Dolomite —a siliceous magnesium limestone. Soil is Clarkville gravelly loam which is low in fertility.

Collections were made from each community at approximately weekly intervals from each of the following strata: Soil, leaf, herb, shrub and tree.

In the oak-hickory community the leaf stratum was composed largely of oak and hickory leaves. In the cedar community this stratum was composed entirely of needles from the cedars, most of which had rotted to a state resembling barnyard manure. This stratum in both communities was about 2 inches deep. The average height of the herb stratum in the oak-hickory community was about 2 feet and the estimated coverage about 90 per cent. The shrub stratum in the oak-hickory community averages about 4.5 feet in height and the estimated coverage was about 45 per cent. The average collecting stroke was about 4 feet high. Estimated coverage of the tree stratum in this community was about 65 per cent. Trees could be swept as high as 12 feet but the average stroke was about 9.5 feet high. In the cedar community only the cedars were swept in each stratum. Each stratum in this community was swept about the same distance from the forest floor as in the oak-hickory community. Estimated coverage of the cedars was about 65 per cent.

In all three vegetation strata in both communities the sweep net method of sampling was used for determining the invertebrate population. Fifty strokes were used with an 18-inch net. The unit used for the soil sample was one square foot taken to a depth of 3 inches and the leaf stratum comprised the dead leaves and debris which covered this area. Soil and leaf samples were multiplied by 11 to bring them to the standard of one square meter for comparison with fifty sweeps of vegetation. All samples were sorted in the laboratory for invertebrates that might be present.

At times, because of the scanty coverage in both communities in the shrub and tree strata, the strokes were not continuous but somewhat scattered. In order to prevent the animals from escaping, between such discontinuous or scattered strokes, the net was quickly closed by placing the hand tightly around the mouth. More effort and care were required to collect from the shrubs than from the herbs and even more in collecting from the trees. Wielding the net above the head, stretching and straining of the body and arms and using a longer net handle all became necessary in collecting from trees. This not only makes collecting from the trees more difficult and tiresome but it is also possible that a larger number of the animals escape from the net. This is true because the strokes cannot be made as rapidly or with as much vigor, since the net is farther away from the collector and not as well under his control as in the lower strata. The writer feels, in general, that the higher the stratum the less efficient is the method of collection. However, no correction factor has been used for this apparent inefficiency of method in the shrub and tree strata.

Temperatures were recorded by ordinary standard thermometers and maximum-minimum thermometers. Readings of relative humidity were made by the cog psychrometer.

In the oak-hickory community the mean temperature for the entire period of study (April 25 to December 1, inclusive) was practically the same in both the soil and leaf strata, being 60.8° F. in the former and 60.3° F. in the latter (Fig. 1). For the entire period of study the mean temperature for the three vegetation strata was also practically the same, being 63.5° F., 63.3° F. and 63.07° F. respectively in the herb, shrub, and tree strata. Although the mean temperatures of the soil and leaf strata were very close and those of the three vegetation strata were also close, this must not be taken as an indication that either the individual readings or the mean monthly temperatures

followed the same trend for the entire period of study. In fact, this was not the case. Although some of the mean monthly temperatures were close to the mean for the entire period the variations for the most part were greater.

It should also be noted that in the three vegetation strata, when the mean monthly temperatures of any two of the strata were close, the third was almost invariably different, being either higher or lower. There is an indication here of the shifting of physical factors from one stratum to another which in turn influenced temperature. The temperature of the three vegetation strata remained somewhat closer together than the temperature of the soil and leaf strata. This is

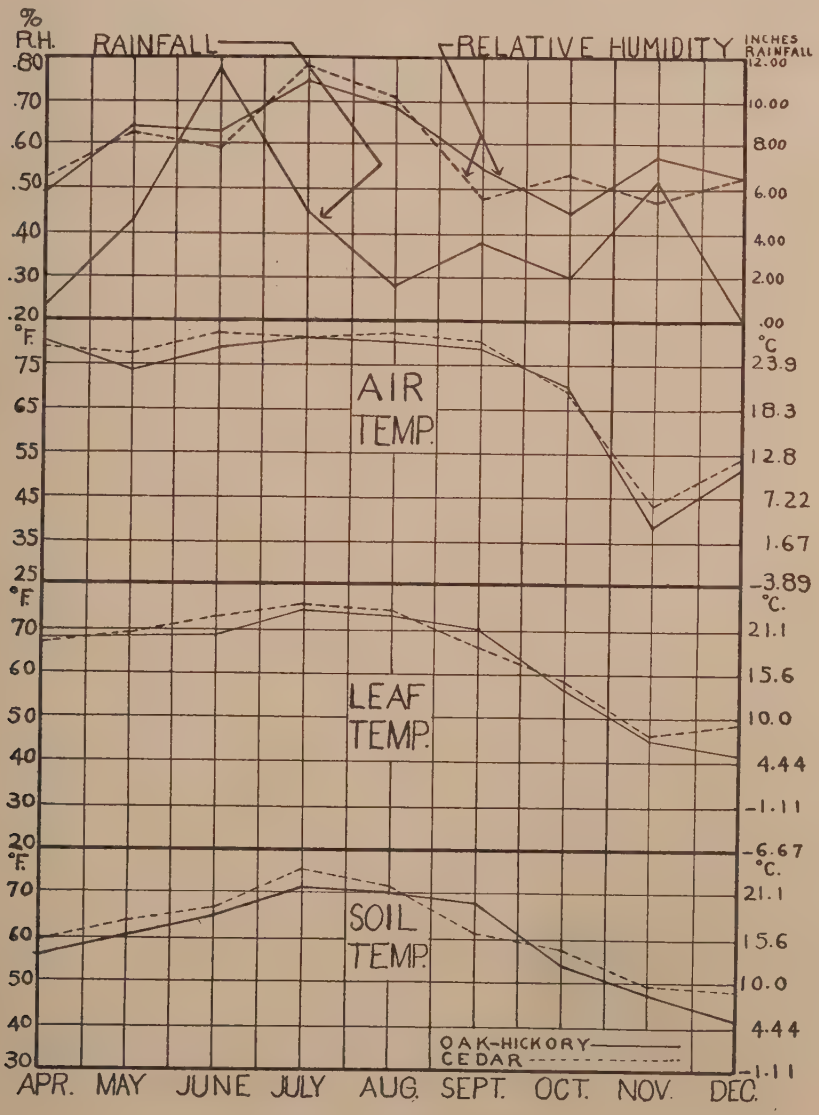

FIG. 1. Meteorological data.

probably because of the greater circulation and consequent mixing of the air above the surface.

Since only standard readings of temperature were taken in the cedar community any comparison of temperature of the two communities will be limited to temperatures taken by the ordinary standard thermometer in both communities. In the cedar community the mean temperature of the soil and leaf strata for the entire period of study was 61.4° F. and 64.07° F. respectively. The difference in temperature of the soil and leaf layers in the cedar community was greater than in the oak-hickory community. This was true for the entire period as well as for the monthly averages. Air temperature in the cedar community was 72.1° F. This was higher than either the herb, shrub, or tree temperature in the oak-hickory community.

Mean relative humidity in both communities was practically the same, being 59 per cent in the oak-hickory and 58.3 per cent in the cedar community (Fig. 1).

Total rainfall was 29.65 inches (Fig. 1).

Vegetation

In the oak-hickory community the following plants are listed in order of greatest coverage in the herb stratum: broom sedge (*Andropogon virginicus* Linn.), horse nettle (*Solanum carolinense* Linn.), golden rod (*Solidago radula* Nutt.), wire grass (*Aristida oligantha* Michx.), horsemint (*Monarda citriodora* Cerv.), purplish cudweed (*Gnaphalium purpureum* Linn.), asters (*Aster ericoides* Linn. and *A. anomalus* Engelm.), and American bell flower (*Campanula americana* Linn.).

The following in the shrub stratum are listed in the same order: Japanese honeysuckle (*Lonicera japonica* Thunb.), white oak (*Quercus alba* Linn.), shagbark hickory (*Carya ovata* K. Koch), and hawthorn (*Crataegus* sp.).

In the tree stratum many of the oaks and hickories were as tall as 80 feet. The following tabulations were made on one acre: white oak (*Quercus alba* Linn.), 84 between four and eight inches in diameter; shagbark hickory (*Carya ovata* K. Koch), 44 between four and eight inches in diameter, and 4 twenty inches in diameter; black walnut (*Juglans nigra* Linn.), 4 between four and eight inches in diameter; bur oak (*Quercus macrocarpa* Michx.), 8 between four and eight inches in diameter; bitternut hickory (*Carya cordiformis* K. Koch), 16 two to four inches in diameter, and 4 from four to eight inches in diameter; American elm (*Ulmus americana* Linn.), 4 between four and eight inches in diameter.

Cedars ranged from a few feet to about 30 feet tall and many of the larger ones were from eight to twelve inches in diameter with their lower limbs almost touching the ground. They were not so evenly distributed as the trees in the oak-hickory community but grew mostly in bunches or clusters. Between these clusters stood the grass (*Andropogon virginicus* Linn.). Species of vegetation are more limited in the cedar community than in the oak-hickory. This is especially true of the dominants of which the red celar is the only one.

In the oak-hickory community there were many rotten logs in various stages of decay. Some had practically gone into humus. In many of these well decayed logs, which had turned into a dry powder-like substance, were numerous pits of ant lions. The latter were identified as *Chrysopa plorobunda* Fitch. A total of 60 logs was counted on one acre, including twelve white oak logs over eighteen inches in diameter. Most of the logs were in the last stage of decay and could not be identified.

The Animal Population

The first collection was made on April 25 and the last on December 1. The animal population (Fig. 2) will now be discussed in greater detail beginning with the collections of the month of April.

April. Only two collections were made in this month, one on the 25th and the other on the 30th. On the 25th, the green

vegetation had begun to appear. The mean air temperature in the oak-hickory community for the last half of the month as recorded in the shrub stratum, 4 feet from the forest floor, was 66.7° F. the relative humidity 52 per cent, and the rainfall 0.7 of an inch. The maximum air temperature was 92° F. and the minimum 44° F. In the two collections in the oak-hickory community a total of 221 animals was collected from the five strata with the following number being taken from each stratum: soil 77, leaf 88, herb 10, shrub 38 and tree 8. More than half

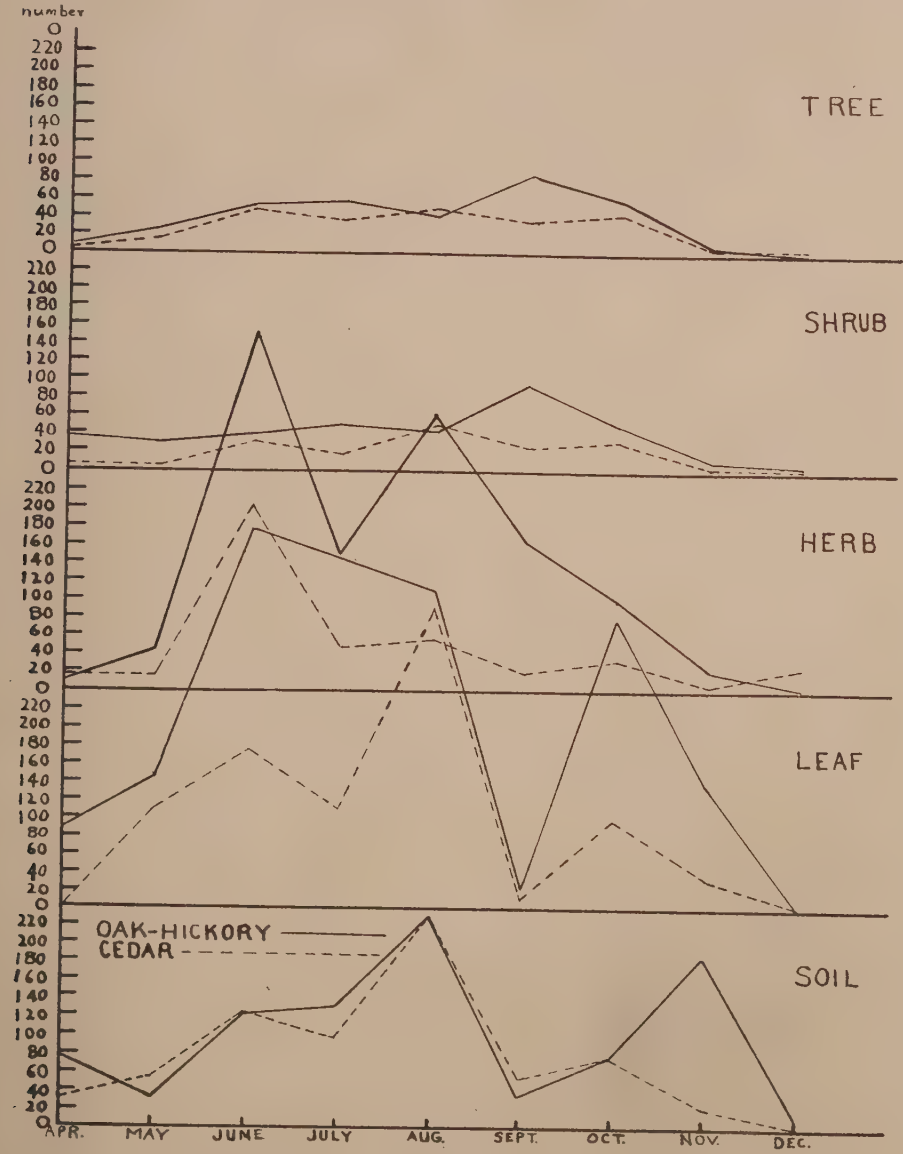

FIG. 2. The animal population. (Two collections in April and November, three in September, one in December, and four in all other months.)

of the fauna taken from the soil and leaves were beetle larvae. The two collections from the cedar community yielded only 59 specimens: soil 33, herb 18, shrub 4 and tree 4.

May. In the oak-hickory community a total of 274 specimens was taken in four collections, a decrease compared with the two collections in April. The number taken from each stratum follows: soil 33, leaf 143, herb 44, shrub 30 and tree 24. Most of the fauna from the leaf stratum were beetles and ants. In the cedar community a total of 201 was collected, an increase over the two collections in April. The number taken in each stratum was: soil 55, leaf 110, herb 18, shrub 2 and tree 16. Beetles and ants were also the most numerous in the cedar community, taken mostly in the leaf stratum. The very definite increase in the leaf stratum in both communities is an indication that because of seasonal changes the invertebrates were becoming more active and tending to move upward.

June. During this month when the peak in population was reached in the oak-hickory community, 1021 were collected. The total population was greatly influenced by ants, spiders, and beetles in the leaf stratum and by the bug, *Oedancala dorsalis* and ants in the herbs. The number from each stratum of the oak-hickory community follows: soil 121, leaf 418, herb 388, shrub 40 and tree 54. From the cedar community a total of 581 was collected, and the following number was taken from each stratum: soil 121, leaf 176, herb 202, shrub 34 and tree 48. Spiders and rove beetles from the soil and diverse groups of Insecta greatly influenced the total population in the cedar community. The largest number was taken from the oak-hickory community in the herb stratum since the collections started on April 25. There was also an increase in the herb stratum in the cedar community. This indicates that the invertebrates were moving upward to the higher strata. It should be noted that a larger number was collected in the trees of both communities than in the shrubs. The mean air temperature in the shrub stratum of the oak-hickory community for the month was 71.7° F.

July. The total population in the oak-hickory community decreased to 775 with the following number being taken from each stratum: soil 132, leaf 385, herb 152, shrub 48 and tree 58. The population in the cedar community also underwent a reduction to 311 with the number from each stratum as follows: soil 99, leaf 110, herb 46, shrub 18 and tree 38. A general reduction occurred in both communities. The increase in temperature probably had much to do with the reduction in population and there is little doubt that it influenced the general decrease in the three vegetation strata and the increase in the soil and leaf strata. However, in both communities a larger number was collected in the tree stratum than in the shrub. The mean monthly temperature in the shrub stratum of the oak-hickory community was 76.1° F.

August. The total number of specimens in both communities increased during this month. In the oak-hickory community 969 and in the cedar community 715 were collected. In the oak-hickory community the total number from each stratum follows: soil 231, leaf 352, herb 300, shrub 44 and tree 42. In the cedar community the number taken in each stratum follows: soil 231, leaf 330, herb 56, shrub 48 and tree 50. The population peak was reached in the cedar community during this month. Again the tree stratum exceeded the shrub stratum in the number of specimens in one community, the cedar, and in the other it was practically the same as in the shrubs. The total population in the oak-hickory community was influenced by the increase of earthworms, beetle larvae, and rove beetles in the soil stratum, by ants, spiders and rove beetles in the leaf stratum, and by the bug, *Oedancala dorsalis,* in the herbs. In the cedar community the increase was augmented by ants, millipedes and beetle larvae in the soil, and by flies,

centipedes, and ants in the leaf stratum. The mean temperature for August had decreased about 2° F. below that of July and the rainfall had also decreased.

September. The total number of specimens in both communities decreased markedly perhaps because of seasonal changes. With the exception of spiders, all invertebrates which had greatly influenced the population in the oak-hickory community during August had been reduced to zero. Likewise the most numerous groups in the cedar community in August were totally absent in this same community during September with the exception of millipedes. In the three collections the total number taken in the oak-hickory community was 393 and in the cedar community 148. The number taken from each stratum in the oak-hickory community was as follows: soil 33, leaf 22, herb 158, shrub 94 and tree 86; in the cedar community the collections were: soil 55, leaf 11, herb 20, shrub 24 and tree 38. In the cedar community the number in the tree stratum is much in excess of the number in the herb or shrub strata. The mean monthly air temperature in the shrub stratum of the oak-hickory community was 70.3° F.

October. In both communities the population increased over that of September. The total number was influenced by the increase of the following forms in the leaf stratum: beetles, beetle and dipterous larvae, ants, centipedes and millipedes. Spiders and various Homoptera and Hemiptera had also increased in the vegetation strata. The total collected in the oak-hickory community was 608, divided as follows: soil 77, leaf 319, herb 100, shrub 52 and tree 60. In the cedar community the total number was 287 showing the following breakdown: soil 76, leaf 99, herb 34, shrub 34 and tree 44. It should be noted that a larger collection in both communities was taken in the tree stratum than in the shrub, and in addition in the cedar community, a larger number was taken in the trees than in the herbs. The mean air temperature was low. In the shrub stratum of the oak-hickory community the air temperature was 54.2° F. and it was practically the same in the herbs. But in the trees it was about 1° F. lower. However, it appears that temperature and other physical factors were not unfavorable to an increase in the highest stratum, the trees. Perhaps the exposure to this reduced temperature had not been of sufficient duration to influence a downward movement of the arthropod fauna.

November. Only two collections were made. In the oak-hickory community the population increased. In the cedar community the reverse was true. In the former community a total of 353 was collected and in the latter only 65. In the oak-hickory community the following number was taken in each stratum: soil 187, leaf 132, herb 20, shrub 10 and tree 4. In this community the increase of beetles in the soil and of earthworms and spiders in the leaf stratum greatly aided in the general increase. In the cedar community the number follows: soil 22, leaf 33, herb 4, shrub 2 and tree 4. The decrease in the cedar community was general, the numbers being smaller in all strata. On account of the general increase in the soil and leaf strata and the decrease in the shrubs and trees, there is reason to believe that the animals were descending to the soil and leaf strata where they might hibernate during the winter. Probably the reduction in temperature had much to do with the shift in population to the lower strata. The mean air temperature in the shrub stratum of the oak-hickory community was now 54.2° F.

December. Only one collection was made this month. In the collection on December 1, 15 arthropods were collected in the oak-hickory community and 26 in the cedar community. In the former community 11 were collected from the soil and 4 from the shrubs; in the latter community 22 were collected in the herb stratum and 4 from the trees. The mean temperature was 39.5° F. Low tem-

peratures had greatly influenced the reduction in population.

The Orders of Arthropoda

Details of the observed stratification will now be discussed. A complete list of species is given in the Appendix.

Pseudoscorpionida

A total of 121 specimens was taken in the leaf stratum of the oak-hickory community. They were not found in any other place. All specimens were of one species, *Dactylochelifer copiosus* Hoff.

Phalangida

Only a few specimens of one species were taken. These were collected in the herb, shrub, and tree strata of both communities. The species was *Leiobunum crassipalpis* Banks.

Araneida

A total of 887 specimens was collected in both communities, 538 in the oak-hickory and 349 in the cedar community. The population peak was reached in the leaf stratum of both communities. With the exception of the soil, spiders show a very wide distribution, with appreciable numbers in all strata studied, as the following data will show: oak-hickory community—soil 22, leaf 286, herb 96, shrub 78, and tree 56; cedar community—leaf 177, herb 82, shrub 50 and tree 40. It should be noted that most of the spiders were taken in the leaf stratum; most of the insects were also found in the leaf stratum. Since spiders prey on insects, they probably inhabited that stratum in largest numbers in order to obtain food. According to Lowrie (1942), however, many spiders live on the substratum because they show a positive reaction to moisture and a negative reaction to high temperature. The species were distributed among the strata as follows: oak-hickory community—soil 2, leaf 13, herb 25, shrub 17, tree 16; cedar community—leaf 5, herb 19, shrub 8, tree 8. A net total of 38 species was taken in the oak-hickory and 28 in the cedar community.

The total number of species taken in the strata of a given community usually exceeded the actual number taken in the community since many species occur in more than one stratum and hence were counted more than once.

Diplopoda

In the oak-hickory community 44 specimens were taken from the soil and 99 from the leaf stratum. In the cedar community the distribution was as follows: soil 165, leaf 66, herb 6, shrub 6. Two species were taken in each community.

Chilopoda

The population peak of this group was reached in the soil where 99 were taken in each community; 77 were also taken in each community from the leaf stratum. None were collected in the herb stratum but a few were taken from the shrubs and trees in each community. Five species were taken in the oak-hickory and 4 in the cedar community.

Orthoptera

The peak in population was reached in the herb stratum in both communities; 84 were taken from the oak-hickory and 68 from the cedar community in this stratum. The leaf stratum was second in population with 44 in the oak-hickory and 11 in the cedar community. No specimens were taken from the soil but a few were taken from other strata. Species were distributed as follows: oak-hickory—soil and leaf 1 each, herb 11, tree 1; cedar community—herb 3. A total of 8 species was taken in the oak-hickory and 4 in the cedar community.

Isoptera

A total of 68 termites was taken from the soil in the oak-hickory community. These were *Reticulitermes virginicus* (Banks).

Corrodentia

A small number of specimens was taken. They were collected in the leaves of the

cedar community and in the leaves, shrubs, and trees of the oak-hickory association. Only two species were identified; they were *Caecilius aurantiacus* (Hagen) and *C. posticus* Banks. The two species were taken from the oak-hickory community.

Hemiptera

A total of 592 was collected. They were distributed in the two communities as follows: oak-hickory—leaf 22, herb 374, shrub 77 and tree 18; cedar community—soil 11, leaf 22, herb 32, shrub 10 and tree 26. The peak in population was reached in the herb stratum in both communities. Species were distributed as follows: oak-hickory—leaf 11, herb 11, shrub 8 and tree 10; cedar community—herb 6, tree 4. Altogether 16 species were taken in the oak-hickory and 8 in the cedar community.

Homoptera

The homopterous insects reached their population peak in the herb stratum in both communities; 372 were taken in this stratum in the oak-hickory and 96 in the cedar community. In the soil and leaf strata of the oak-hickory community 22 and 55 were taken respectively but none were taken in the corresponding strata of the cedar community. In the shrub stratum 34 were collected in each community. From the tree stratum 62 were taken in the oak-hickory and 50 in the cedar community. The tree stratum stood second in population in both communities. Species were distributed as follows: oak-hickory—leaf 1, herb 17, shrub 8, tree 10; cedar community—herb 9, shrub 5, tree 5. The species inhabiting the grass were for the most part leafhoppers. The total taken in the oak-hickory association was 27 and in the cedar community, 14. Most homopterous insects were leafhoppers.

Neuroptera

Only a few of this order were taken in the herb, shrub, and tree strata of the oak-hickory association. One species was identified; it was *Chrysopa plorobunda* Fitch.

Diptera

Diptera were limited in species as well as in number of specimens. A total of only 319 was collected in both communities. Distribution in the oak-hickory community was as follows: soil, 22 larvae; leaf, 66 larvae; herb, 44 adults; shrub, 23 adults and 4 larvae; tree, 14 adults and 2 larvae. In the cedar community, the distribution was: soil, 22 larvae; leaf, 33 adults and 11 larvae; herb, 30 adults; shrub, 16 adults; tree, 32 adults. Ten species were taken in the oak-hickory and 3 in the cedar community.

Lepidoptera

This order was limited to larvae with the exception of one adult. The latter was identified as *Exartema fasciatanum* Clem. Larvae were not identified. The peak in population of the larvae was reached in the leaf stratum in both communities. In the oak-hickory community, the larvae were distributed as follows: soil 33, leaf 122, herb 34, shrub 24, and tree 38. In the cedar community the distribution was as follows: leaf 11, herb 18, and tree 12.

Caterpillars (fall webworms, *Hyphantria cunea* (Drury)) were distributed heavily through the oak-hickory community for the most part on the shagbark hickories. The average distance of the web from the ground was approximately 30 feet.

Coleoptera

In the oak-hickory community 1158 Coleoptera were collected, 450 of which were larvae. In the cedar community 572 were collected and of these 114 were larvae. In the oak-hickory community the stratal distribution was as follows: soil, 77 adults and 253 larvae; leaf, 439 adults and 187 larvae; herb, 48 adults; shrub, 54 adults and 8 larvae; tree, 90 adults and 2 larvae. The distribution follows in the cedar community: soil, 110

adults and 66 larvae; leaf 198 adults and 44 larvae; herb, 60 adults; shrubs, 30 adults and 2 larvae; tree, 60 adults and 2 larvae. From the lowest to the highest strata, there is in general a decrease in the larvae and an increase in adults. In the adult stage the population peak in both communities was reached in the leaf stratum. In the oak-hickory community the population peak in the larval stage was reached in the soil but in the cedar community this peak was reached in the leaf stratum. This order shows a very wide distribution through all strata investigated. A larger number was taken in the tree stratum than in the herbs or shrubs. Total stratal distribution of the species was as follows: oak-hickory—soil 1, leaf 7, herb 13, shrub 9, and tree 13; cedar community—herb 9, shrub 4 and tree 11.

It should be noted that in the adult stage the population peak in both communities was reached in the leaf stratum but the largest number of species in the oak-hickory community was taken in the herb and tree strata to the extent of 13 in each. In the cedar community, the largest number, 11, was taken from the trees. A total of 33 species of Coleoptera was taken in the oak-hickory and 23 in the cedar community.

Hymenoptera

A total of 717 Hymenoptera was collected in the oak-hickory community and 400 in the cedar community. Of this total in the former community, 653 were ants while in the latter community only 265 were ants. The stratal distribution in the oak-hickory community was as follows: soil 165, leaf 322, herb 120, shrub 58 and tree 52. In the cedar community the distribution was: soil 120, leaf 210, herb 28, shrub 18 and tree 24. A larger number of ants was collected from the leaf stratum than from the soil. All three vegetation strata in the oak-hickory community yielded a larger number of ants as well as other Hymenoptera than the corresponding strata in the cedar community. Ants show a very wide vertical distribution through all five strata. The population peak of ants and Hymenoptera in general was reached in the leaf stratum of the oak-hickory community and in the soil stratum of the cedar community.

In the oak-hickory community 18 species were taken and in the cedar community 12. The stratal distribution of the species follows: oak-hickory—soil 4, leaf 6, herb 5, shrub 5, and tree 4; cedar community—soil 4, leaf 3, herb 4, shrub and tree 1 each.

In the cedar community a number of qualitative collections were made from a society of grasses, mainly *Andropogon virginicus* Linn. The species taken are listed in the Appendix, and the number of species in each order follows: Araneida, 10; Orthoptera, 1; Hemiptera, 2; Homoptera (mostly leafhoppers), 15; Hymenoptera, 1.

Summary and Conclusions

This study extended from April 25 to December 1, inclusive. The red cedar community is in the developmental stage, perhaps a subclimax of the oak-hickory community, rarely found in low places but usually on slopes or hill sides on rocky areas. The cedar community covers much less ground than the oak-hickory and the trees are not so tall nor so large as the oaks and hickories. A few of the cedars reached a height of about 30 feet and about 12 inches in diameter. In contrast in the oak-hickory community some trees are as tall as 80 feet and as much as 20 inches in diameter. Both communities are secondary ones.

The mean temperature of the two communities for the entire period was as follows: oak-hickory—soil 60.8° F., leaf 60.3° F., air 63.3° F.; cedar community—soil 61.4° F., leaf 64.07° F., air 72.1° F. Relative humidity was about the same in both communities: 59 per cent in the oak-hickory and 58.3 per cent in the cedar community. Soil is the Clarkville grav-

elly loam with low fertility. Rainfall was 29.95 inches.

The total number of specimens taken in each stratum of the oak-hickory community exceeded that of the corresponding stratum of the cedar community as the following figures will show:

Oak-hickory—soil 902, leaf 1859, herb 1172, shrub 360 and tree 336.

Cedar community—soil 692, leaf 869, herb 420, shrub 166 and tree 246.

In both communities the number of specimens from the leaf stratum exceeded those from the soil, the excess being greater in the oak-hickory than in the cedar community.

Further, the above data will show that the numbers of specimens from the two soil strata of the two communities are much more alike than are those from the two leaf strata. More than twice the number, 2.14, was taken from the leaf stratum of the oak-hickory association than from the cedar community; whereas only about 1.3 times as many were found in the soil of the oak-hickory as in the soil of the cedar community.

In regard to the three vegetation strata, the herb stratum yielded the highest number of specimens in both communities.

It should also be noted that in the cedar community a larger number of specimens was taken in the tree than in the shrub stratum; and in the oak-hickory community the shrub stratum exceeded the tree stratum by only 24 specimens.

The shrub and tree strata in each community are much more closely related to each other in number of specimens collected than they are to the herb stratum.

A more accurate comparison of the three vegetation strata of the two communities follows: 2.8 times as many specimens were taken in the herb stratum of the oak-hickory community as in the cedar community; 2.17 times as many in the shrub stratum of the oak-hickory as in the cedar community; and 1.37 times as many in the tree stratum of the oak-hickory as in the cedar community.

In several individual collections the number of specimens in the tree stratum exceeded the number taken in the shrubs and in a few collections it also exceeded the number taken in the herbs.

The oak-hickory community exceeded the cedar community in all monthly collections. The three highest monthly totals in the population in the oak-hickory association occurred as follows: June 1021, August 969, and July 775. The highest in the cedar community were August 715, June 581 and July 311. Thus the highest peaks did not occur during the same month. However, it is worth pointing out that the highest in the oak-hickory and the second highest in the cedar community did occur during the same month. Again the second highest population in the oak-hickory and the highest in the cedar community also occurred the same month.

The order Coleoptera stands first in abundance of specimens in both communities. Hymenoptera is second in the oak-hickory community but the spiders stand second in the cedar community. The third, fourth, fifth, sixth and seventh groups in order of abundance in both communities follow: Spiders, Homoptera, Hemiptera, Diptera and Lepidoptera (all larvae). The groups standing highest in species are as follows: spiders, 38 in the oak-hickory and 28 in the cedar community; Coleoptera, 38 in the oak-hickory and 23 in the cedar community; Homoptera, 27 in the oak-hickory and 14 in the cedar community; Hymenoptera, 18 in the oak-hickory and 12 in the cedar community; Hemiptera, 16 in the oak-hickory and 8 in the cedar community.

In both communities the largest numbers of Coleoptera, spiders and Lepidoptera (larvae) were taken in the leaf stratum, but the largest numbers of Hemiptera and Homoptera were taken in the herb stratum. In the oak-hickory community the largest number of Diptera was taken in the soil but in the cedar community the largest number was taken in the leaf stratum. The largest number of Hymenoptera in the oak-hickory community was

taken from the leaf stratum but in the cedar community the largest number was collected in the soil.

In both communities the herb stratum stands first in yielding the greatest number of species—91 in the oak-hickory association and 55 in the cedar community. In the oak-hickory association, the tree stratum yielded 53 species and in the shrubs 46. In the latter association, 9 species were taken from the soil and 37 from the leaf stratum. In the cedar community the following were taken from the remaining strata: soil 8, leaf 16, shrub 23 and tree 38.

In the society of grasses in the cedar community 40 species were taken, mostly leafhoppers.

The number of species taken in the various strata of the oak-hickory community but not in the corresponding strata of the cedar community follows: soil 3, leaf 30, herb 66, shrub and tree 40 each.

The number of species taken in the strata of the cedar community but not in the corresponding strata of the oak-hickory: soil 4, leaf 8, herb 27, shrub 18 and tree 27.

The number of species taken in the corresponding strata of both communities: soil 4, leaf 6, herb 27, shrub 5, and tree 8.

The number of species taken in the oak-hickory community but not taken in the cedar community was 102. The number taken in the cedar community but not taken in the oak-hickory was 38.

The number of species taken in or limited to only one stratum was: oak-hickory 111, cedar 75; limited to two strata—oak-hickory 30, cedar 14; limited to three strata—oak-hickory 18, cedar 5; limited to four strata—oak-hickory 2, cedar 2. None were taken in all five strata.

A total of 27 collections was made in each community and in each stratum, collecting a total of 4,629 animals in the oak-hickory and 2,393 in the cedar community, almost twice as many in the former as in the latter, to be specific 1.93 times as many in the oak-hickory as in the cedar community. The total number of species taken in the oak-hickory community was 164. The total number taken in the cedar community was 99.

The foregoing data seem to justify the following conclusions on stratification:

1. A larger number of specimens and species was taken in each stratum of the oak-hickory association than in the corresponding stratum of the cedar consocies, but the basic pattern of stratification is the same in both communities.

2. Variation in temperature and other physical and biological factors from one level to another probably form the basis for stratal societies.

3. Variation in quantity and quality in the arthropod fauna from one level or from one stratum to another appears to justify the concept of stratification.

4. The population peak in stratal societies was reached in the leaf stratum in both communities with a general decrease in the strata above and below the leaf stratum. However, if we compare only the three vegetation strata, the peak was reached in the herbs.

5. Both food and shelter are probably very important in determining the stratal position of the population peak during the warmer periods of the year. Shelter alone might be very important in this respect during the colder periods. The trees exceeded the shrubs in animal population in the cedar community. In the oak-hickory association the shrubs exceeded the trees by only 24 specimens. The tree stratum also exceeded the shrub stratum in species in both communities. Even to the casual observer the trees were more numerous and afforded greater coverage than the shrubs and hence more shelter for hiding, breeding, and feeding in the tree stratum than in the shrubs. This was also obvious in the herbs which had a greater coverage than either of the vegetation strata and hence stood first in specimens and species in both communities.

6. The tree stratum is more important than is usually indicated and more re-

search should be directed toward this stratum.

7. Species of certain orders of Arthropoda show a wider distribution through all five strata than others, for example, Coleoptera, Araneida and Formicidae.

8. The species composition of the stratal societies were different within the same community as well as between the two communities.

9. No species were taken in all five strata. The numbers of species taken which range through four strata were as follows: oak-hickory 2, cedar 2; the number taken or limited in three strata—oak-hickory 18, cedar 5; taken in or limited to two strata—oak-hickory 30, cedar 14; limited to one stratum—oak-hickory 111, cedar 75.

Appendix

A list of the species identified. The table shows the number, the community and the stratum from which each species was taken. Oak H = oak-hickory community; Cedar = cedar community; Grass = a society of grasses in the cedar community.

Arachnida

Pseudoscorpionida. Cheliferidae. *Dactylochelifer copiosus* Hoff. Oak H: leaf 66. **Phalangida.** Phalangiidae. *Leiobunum crassipalpis* Bks. Oak H: herb 21, shrub 2, tree 2. Cedar: herb 2, shrub 2, tree 2. **Araneida.** Dictynidae. *Dictyna sublata* Hentz. Oak H: leaf 33, herb 2, shrub 12, tree 8. *Dictyna* sp. Cedar: herb 2. Linyphiidae. *Ceraticelus* sp. Oak H: shrub 2. *Ceratinopsis* sp. Oak H: herb 1. *Ceratinops crenata* Em. Cedar: leaf 22. *Frontinella communis* Hentz. Cedar: herb 2, grass 1. *Linyphia marginata* C. Koch. Oak H: leaf 22. Cedar: grass 1. *Meioneta* sp. Oak H: leaf 22. Cedar: grass 2. *Origanates rostratus* Em. Oak H: soil 22. Argiopidae. *Acanthepeira stellata* Walck. Oak H: herb 2. *Aranea displicata* Hentz. Oak H: tree 4. Cedar: leaf 11. *Aranea forata* Keys. Cedar: tree 2. *Eustala anastera* Walck. Oak H: herb 2, shrub 2, tree 2. Cedar: tree 8. *Larinia directa* Hentz. Cedar: herb 2, grass 4. *Leucauge venusta* Walck. Oak H: herb 2. Cedar: herb 2, tree 2. *Mangora gibberosa* Hentz. Oak H: herb 1. Cedar: herb 1. *Mangora placida* Hentz. Oak H: herb 14, tree 2. Cedar: herb 6, grass 4. *Neoscona benjamina* Walck. Oak H: herb 2. Cedar: tree 2. *Singa nigripes* Keys. Oak H: shrub 4, tree 2. Cedar: leaf 11, herb 2, shrub 2. *Tetragnatha laboriosa* Hentz. Cedar: grass 2, shrub 3. *Tetragnatha* sp. Cedar: leaf 22, grass 3. *Verucosa arenata* Walck. Oak H: tree 2. *Wixia ectypa* Walck. Oak H: shrub 2. Mimetidae. *Ero leonina* Hentz. Oak H: herb 2. *Mimetus* sp. Cedar: herb 2. Agelenidae. *Agelenopsis* sp. Cedar: herb 2. Pisauridae. *Dapanus mirus* Walck. Oak H: herb 6. Lycosidae. *Lycosa punctulata* Hentz. Cedar: grass 2. Oxyopidae. *Oxyopes salticus* Hentz. Oak H: leaf 11, herb 2. Cedar: grass 3, tree 2. *Oxyopes scalaris* Hentz. Cedar: shrub 2, tree 1. Thomisidae. *Ebo latithorax* Keys. Cedar: herb 1. *Misumenops asperatus* Hentz. Oak H: herb 8, shrub 2, tree 1. Cedar: herb 6, grass 2, shrub 2. *Philodromus inaequipes* Bks. Oak H: herb 1, shrub 4, tree 2. Cedar: leaf 11. *Philodromus rufus* Walck. Oak H: shrub 11. *Philodromus* sp. Oak H: shrub 11, tree 11. *Tmarus angulatus* Walck. Oak H: herb 2, tree 2. *Xysticus ferox* Hentz. Oak H: leaf 11, herb 2. Cedar: herb 1. *Xysticus funestus* Keys. Oak H: leaf 11, herb 4. Cedar: herb 1. Clubionidae. *Anyphaena* sp. Oak H: shrub 2. *Phrurotimpus emertoni* Gertsch. Oak H: leaf 33. *Phrurotimpus palustris* Bks. Oak H: leaf 11. *Wulfila saltabunda* Hentz. Oak H: herb 2, shrub 2. Cedar: herb 2. Gnaphosidae. *Drassyllus aprilinus* Bks. Oak H: leaf 55. *Drassyllus* sp. Oak H: leaf 22. Cedar: leaf 11. *Zelotes duplex* Chamb. Oak H: soil 11, leaf 11, tree 2. Cedar: herb 1. Salticidae. *Evarchi hoyi* Pckm. and Pckm. Cedar: grass 2. *Hentzia palmarum* Hentz. Oak H: herb 2, shrub 1, tree 6. *Maevia vittata* Hentz. Oak H: herb 2, shrub 2. Cedar: shrub 3. *Metaphidippus flavipedes* Pckm. and Pckm. Oak H: herb 2, shrub 3. Cedar: herb 7, shrub 24, tree 24. *Metaphidippus protervus* Walck. Oak H: herb 4, shrub 8, tree 9. Cedar: herb 1, grass 1, tree 1. *Paraphidippus marginatus* Walck. Oak H: tree 2. *Peckhamia picata* Pckm. and Pckm. Oak H: herb 1, tree 1. *Phidippus clarus* Keys. Oak H: herb 3. *Phidippus insolens* Hentz. Oak H: leaf 11, herb 12. Cedar: herb 1, grass 2, shrub 2. *Phidippus* sp. Oak H: leaf 11, herb 1. Cedar: herb 4, grass 4, shrub 2, tree 1. *Thiodina sylvana* Hentz. Oak H: herb 2, shrub 2, tree 1.

Diplopoda

Polydesmidae. *Fontaria subterraneous* Hefner. Oak H: soil 88. Cedar: soil 165. Julidae. *Parajulus impressus* Say. Oak H: leaf 99. Cedar: leaf 33, herb 6, shrub 6.

Chilopoda

Dicellophilidae. *Dicellophilus limatus* Wood. Oak H: soil 99, tree 3. Cedar: soil 99, shrub 6. Lithobiidae. *Lithobius bilabiatus* Wood. Oak H: leaf 11. *Lithobius forficatus* Linn. Oak H: leaf 11. *Lithobius lundi* Meinert. Oak H: herb 6, shrub 7, leaf 11. Cedar: leaf

33. *Lithobius pullus* Boll. Cedar: leaf 22. *Lithobius trilobius* Boll. Oak H: leaf 22. Cedar: leaf 44.

INSECTA

Orthoptera. TETTIGONIIDAE. *Amblycorypha huasteca* (Sauss.). Oak H: herb 1. *Amblycorypha* sp. Cedar: herb 1. *Microcentrum rhombifolium* (Sauss.). Oak H: herb 3. *Orchelimum* sp. Oak H: tree 10. *Scudderia* sp. Oak H: herb 1. TETRIGIDAE. *Tettigidae lateralis* (Say). Oak H: herb 1. Cedar: herb 2. GRYLLIDAE. *Hapithus agitator* Uhler. Oak H: herb 1. *Oecanthus latipennis* Riley. Oak H: herb 3. ACRIDIDAE. *Chloealtis conspersa* Harris. Oak H: herb 3. *Chortophaga viridifasciata* DeGeer. Cedar: grass 1. *Dichromorpha viridis* (Sc.). Oak H: herb 2. *Melanoplus femurrubrum* DeGeer. Oak H: herb 10. Cedar: herb 14, grass 1. *Melanoplus gracilis* (Bruner). Oak H: herb 1. *Melanoplus* sp., *gracilis?* Cedar: herb 2. BLATTIDAE. *Parcoblatta lata* Brunner. Oak H: leaf 11. **Isoptera.** TERMITIDAE. *Reticulitermes virginicus* (Bks.). Oak H: leaf 66. **Corrodentia.** PSOCIDAE. *Caecilius aurantiacus* Hagen. Oak H: shrub 2. **Hemiptera (Heteroptera).** MIRIDAE. *Hyaliodes harti* Knight. Oak H: shrub 3. *Lygus oblineata* (Say). Oak H: herb 3. Cedar: herb 1, grass 1. *Parthenicus juniperi* (Heidemann). Oak H: tree 1. *Pilophorus juniperi* Knight. Oak H: herb 1. NABIDAE. *Nabis roseipennis* Reuter. Oak H: herb 3. *Nabis ferus* (L.). Cedar: tree 1. REDUVIIDAE. *Zelus socius* Uhler. Cedar: tree 1. *Zelus exanguis* Stal. Oak H: shrub 1, tree 2. TINGIDAE. *Corythucha cydoniae* (Fitch). Oak H: tree 3. *Gargaphia solani* Heidemann. Oak H: herb 1. LYGAEIDAE. *Cymus angustatus* Stal. Oak H: herb 6. *Geocoris uliginosus* (Say). Oak H: herb 1. *Myodocha serripes* Oliv. Oak H: leaf 11. *Oedancala dorsalis* (Say). Oak H: herb 240, shrub 5, tree 5. Cedar: herb 12. *Phlegyas abbreviatus* (Uhler). Oak H: herb 16, shrub 8. Cedar: herb 21, tree 1. NEIDIDAE. *Jalysus spinosus* (Say). Oak H: herb 23, shrub 5, tree 1. Cedar: leaf 22, herb 2. COREIDAE. *Leptoglossus oppositus* (Say). Oak H: shrub 1. PENTATOMIDAE. *Corimelaena pulicaria* (Germ.). Cedar: herb 8. *Euchistus variolarius* P. deB. Oak H: herb 4, shrub 15. *Euchistus tristigmus* (Say). Oak H: leaf 22. Cedar: grass 1. *Mormidae lugens* (F.). Oak H: herb 16, shrub 1. Cedar: grass 1, tree 1. *Podisus maculiventris* (Say). Oak H: herb 2, shrub 7, tree 1. Cedar: tree 3. **(Homoptera).** CERCOPIDAE. *Clastoptera arborina* Ball. Oak H: herb 1. *Clastoptera xanthocephala unicolor* Fowler. Cedar: herb 2, shrub 6, tree 4. *Lepyronia quadrangularis* (Say). Oak H: herb 9. Cedar: herb 1, grass 11. MEMBRACIDAE. *Acutalis nigrinervis* (Fowler). Cedar: grass 2. *Campylenchia latipes* (Say). Oak H: herb 2. Cedar: shrub 2. *Cyrtolobus funkhouseri* Woodruff. Oak H: herb 1. *Entylia concisa* Walk. Oak H: herb 3. *Publilia reticulata* Van D. Oak H: herb 212, shrub 3, tree 5. Cedar: herb 2, grass 4, tree 2. *Stictocephala inermis* (F.). Cedar: grass 1. CICADELLIDAE. *Acinopterus acuminatus* Van D. Oak H: tree 1. Cedar: tree 1. *Acertagallia sanguinolenta* (Prov.). Cedar: grass 1. *Aulacizes irrorata* (F.). Oak H: herb 2, shrub 5. Cedar: herb 4, grass 2. *Chlorotettix galbanatus* Van D. Cedar: grass 1. *Chlorotettix tunicatus* Ball. Oak H: herb 4. Cedar: grass 3. *Chlorotettix lusorius* O. & B. Oak H: shrub 3. *Chlorotettix* sp. Oak H: herb 3. *Doleranus longulus* (G. & B.). Oak H: shrub 3. *Draeculacephala mollipes* (Say). Oak H: leaf 11, herb 5. Cedar: herb 3, grass 1. *Empoasca* sp. Oak H: tree 2. *Endria inimina* (Say). Oak H: herb 9. Cedar: grass 6, tree 3. *Erythroneura* sp. Oak H: herb 4, shrub 3, tree 6. *Graminella nigrifrons* (Forbes). Cedar: grass 3. *Graphocephala coccinea* (Först.). Oak H: herb 5, shrub 3. Cedar: herb 8. *Idiocerus nervatus* Van. D. Cedar: herb 8, tree 4. *Idiocerus* sp., *alternatus* complex? Cedar: shrub 12. *Japananus hyalinus* (Osb.). Oak H: tree 3. *Laevicephalus acus* (S. & DeL.). Oak H: herb 3. *Menosoma cincta* (O. & B.). Oak H: tree 3. *Neokolla hieroglyphica* (Say). Oak H: shrub 4. *Paraphlepsius irroratus* (Say). Oak H: soil 99, leaf 99, herb 175, tree 10. Cedar: herb 6, grass 12, tree 10. *Polyamia weedi* (Van D.). Oak H: herb 2. *Stirellus obtutus* (Van D.). Oak H: herb 2. Cedar: grass 2. *Texananus superbus* (Van D.). Cedar: grass 2, herb 3. *Tylozygus bifidus* (Say). Oak H: shrub 2. ACANALONIIDAE. *Acanalonia bivittata* (Say). Oak H: herb 1, tree 1. Cedar: herb 6, grass 1, shrub 1, tree 1. DERBIDAE. *Apache degerii* (Kby.). Cedar: shrub 2. *Syntames uhleri* (Ball). Oak H: herb 1, tree 3. CIXIIDAE. *Pintalia dorsivittata* (Van D.). Oak H: tree 4. ACHILIDAE. *Catonia impunctata* (Fh.). Oak H: tree 3. DELPHACIDAE. *Delphacodes campestris* (Van D.). Oak H: herb 2. **Neuroptera.** CHRYSOPIDAE. *Chrysopa plorobunda* Fitch. Oak H: herb 2, shrub 1, tree 1. **Diptera.** FUNGIVORIDAE. *Neoempheria illustris* Joh. Cedar: grass 1. BIBIONIDAE. *Bibio longipes* Lw. Oak H: herb 22. Cedar: herb 3, shrub 2, tree 2. SYRPHIDAE. *Paragus tibialis* (Fallen). Cedar: shrub 2. HELEOMYZIDAE. *Suillia quinquepunctata* (Say). Oak H: tree 1. OTITIDAE. *Tritoxa incurva* Lw. Oak H: herb 8. DROSOPHILIDAE. *Drosophila repleta* Woll. Oak H: herb 1. *Drosophila simulans* Sturt. Oak H: shrub 2. CHLOROPIDAE. *Hippelates bishoppi* Sabr. Oak H: shrub 4. *Madiza trigramma* (Lw.). Oak H: herb 3. *Madiza quadrivittata* Sabr. Oak H: herb 1. *Oscinella*

carbonaria (Lw.). Cedar: grass 32. *Pseudogaurax signatus* (Lw.). Cedar: herb 1. MUSCIDAE. *Coenosia atrata* Walk. Cedar: grass 33. CALLIPHORIDAE. *Phaenicia caeruleviridis* (Macq.). Oak H: leaf 11. SARCOPHAGIDAE. *Sarcophaga rapax* Walk. Cedar: grass 6. *Sarcophaga galeata* Ald. Oak H: herb 4. **Lepidoptera.** OLETHREUTIDAE. *Exartema fasciatanum* Clem. Oak H: herb 2. **Coleoptera.** CARABIDAE. *Anisodactylus dulcicollis* Laf. Oak H: leaf 11. *Lebia lobulata* Lec. Oak H: leaf 11. *Notiophilus novemstriatus* Lec. Cedar: soil 11. LAMPYRIDAE. *Photinus* sp., near *pyralis* (L.). Oak H: herb 1. CANTHARIDAE. *Tytthonyx erythrocephala* (F.). Oak H: tree 1. Cedar: tree 1. *Trypherus latipennis* (Germ.). Oak H: herb 1. Cedar: herb 1. MORDELLIDAE. *Glipodes sericans* (Melsh.). Oak H: tree 1. *Mordellistena trifasciata* (Say). Cedar: herb 2. ANTHICIDAE. *Notoxus bicolor* (Say). Oak H: shrub 2. *Tomoderus interruptus* Laf. Oak H: leaf 55. BUPRESTIDAE. *Agrilus* sp. Cedar: tree 2. *Pachyscelus laevigatus* (Say). Oak H: herb 10. HELODIDAE. *Ptilodactyla serricollis* (Say). Oak H: soil 11. NITIDULIDAE. *Epuraea rufa* (Say). Oak H: leaf 11. *Glischrochilus quadrisignatus vera* (Say). Cedar: herb 2. CUCUJIDAE. *Oryzaephilus surinamensis* (L.). Cedar: shrub 2. CRYPTOPHAGIDAE. *Loberus impressus* Lec. Cedar: tree 1. *Tomarus pulchellus* Lec. Cedar: tree 3. LATHRIDIIDAE. *Melanophthalma picta* Lec. Cedar: tree 3. COCCINELLIDAE. *Anatis 15-punctata* (Oliv.). Oak H: leaf 11. *Cycloneda immaculata* (F.). Oak H: herb 8. *Psyllobora viginti-maculata* (Say). Oak H: shrub 1. *Scymnus* sp., runs to *innocens* Cys. Oak H: herb 1. Cedar: herb 3, tree 1. *Stethorus punctum* (Lec.). Oak H: tree 3. TENEBRIONIDAE. *Paratenetus cribratus* Mots. Cedar: tree 2. *Platydema excavatum* (Say). Cedar: herb 3. SCRAPTIIDAE. *Canifa plagiata* (Melsh.). Cedar: herb 1, shrub 2. PTINIDAE. *Ptinus texanus* Pic. Cedar: tree 1. SCARABAEIDAE. *Anomala* (*Pachystethus*) *marginata* F. Oak H: tree 2. CHRYSOMELIDAE. *Agroiconota bivittata* (Say). Cedar: grass 1. *Deloyala guttata* (Oliv.). Oak H: leaf 11, shrub 1. *Epitrix humeralis* Dury. Oak H: herb 1. *Glyptina abbreviata* Gent. Oak H: tree 1. *Glyptina cyanipennis* Cr. Oak H: herb 1. *Longitarsus testaceus* Melsh. Cedar: tree 1. *Ochrosis atriventris* (Melsh.). Oak H: tree 1. *Paria canella* (F). Cedar: tree 4. *Paria canella* var. *gilvipes* Cr. Oak H: tree 6. *Paria canella* var. *sexnotata* (Say). Cedar: leaf 154, herb 4, shrub 4, tree 39. *Pachybrachis cephalicus* Fall. Oak H: herb 3. *Phyllobrotica limbata* (F.). Oak H: herb 1. *Saxinis omergera* Lac. Oak H: herb 12. *Xanthonia decemnotata* (Say). Oak H: shrub 1. *Xanthonia villosula* (Melsh.). Oak H: herb 5, shrub 9, tree 1. Cedar: herb 3, shrub 1, tree 1. CURCULIONIDAE. *Anthonomus molochinus* Dietz. Cedar: herb 2. *Apion griseum* Smith. Oak H: herb 4, shrub 3, tree 3. Cedar: tree 1. *Aulobaris naso* Lec. Cedar: tree 3. *Conotrachelus anaglypticus* (Say). Oak H: herb 4. *Conotrachelus naso* Lec. Oak H: leaf 22. *Conotrachelus posticatus* Boh. Oak H: leaf 11. *Curculio baculi* (Chttn.). Oak H: herb 1, tree 1. *Gelus oculatus* (Say). Cedar: tree 3. *Lixus cylvius* Boh. Oak H: herb 3. *Smicronyx* sp. (No data.) **Hymenoptera.** BRACONIDAE. *Microgaster facetosa* Weed. Cedar: herb 3. ICHNEUMONIDAE. *Areolopristomerus dubius* (Brues). Cedar: herb 2. *Charops annulipes* Ashm. Cedar: grass 2. *Mesochorus discitergus* (Say). Oak H: herb 2. *Mesochorus uniformis* Cress. Oak H: herb 3. EULOPHIDAE. *Euplectrus leucotrophis* How. Cedar: herb 1. ENCYRTIDAE. *Chrysopophagus compressicornis* Ashm. Oak H: tree 1. TORYMIDAE. *Torymus dasyneurae* (Huber). Oak H: herb 4. CHALCIDIDAE. *Spilochalcis albifrons* (Walsh). Oak H: herb 2. CYNIPIDAE. *Prosaspicera similis* (Ashm.). Oak H: herb 1. SCELIONIDAE. *Trissolcus euschisti* (Ashm.). Cedar: tree 1. FORMICIDAE. *Aphaenogaster fulva aquia* (Buck.). Oak H: soil 11, leaf 121, herb 7, shrub 6, tree 4. Cedar: soil 11, leaf 33. *Camponotus castaneus americanus* Mayr. Cedar: herb 2. *Camponotus caryae* (Fitch). Oak H: shrub 1. *Camponotus herculeanus pennsylvanicus* (DeGeer). Oak H: herb 2, shrub 8. *Crematogaster lineolata* (Say). Oak H: herb 92, shrub 64, tree 44. Cedar: herb 2, grass 2, tree 2. *Formica pallide-fulva* Latr. Oak H: soil 11, leaf 11, herb 3. Cedar: soil 0. *Formica fusca* var. *subsericea* (Say). Oak H: leaf 11, herb 185, shrub 5, tree 4. Cedar: soil 44, herb 7. *Formica pallide-fulva nitidiventris* Emery. Oak H: herb 10. Cedar: herb 5. *Leptothorax curvispinosus* Mayr. Oak H: leaf 11, shrub 8. Cedar: leaf 11, grass 1. *Myrmecina graminicola americana* Emery. Cedar: soil 11. *Ponera coarctata pennsylvanica* Buck. Oak H: soil 120, leaf 198. Cedar: soil 85, leaf 85, shrub 8. *Prenolepis imparis* (Say). Oak H: soil 1, leaf 1, shrub 1, tree 1. *Stigmatomma pallipes* (Hald.). Oak H: leaf 11. SPHECIDAE. *Stigmus fraternus* (Say). Oak H: tree 1. HALICTIDAE. *Augochlora striata* Prov. Oak H: tree 1.

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CAUSES AFFECTING CHANGE AND RATE OF CHANGE IN A VEGETATION OF ANNUALS IN IDAHO[1]

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INTRODUCTION

Why does one plant community give way to another and at what rate does the change take place? The present paper is concerned mainly with these two questions. The questions deal here with simple communities of annuals and are further limited to conditions under which the influences that delay or upset the continuity of the changes, are eliminated or minimized. Pertinent matter concerning the development of the communities, their order of appearance, their relationships to one another and to some of the physical factors involved are all brought together in order to deal with the above questions. The material is drawn from studies previously published as well as from some that are unpublished. It included results from experiments and also inferences from observations covering many years of study of the various plant communities that form on denuded areas of the Northern shrub-grass type of vegetation in southcentral Idaho. The bearing of these studies on some other phases of ecological knowledge is discussed.

THE COMMUNITIES

Russian-thistle (*Salsola kali* var. *tenuifolia* Taŭsch), mustards, including flixweed (*Descurainia sophia* (L.) Webb) and tumblemustard (*Sisymbrium altissimum* L.) and downy chess (*Bromus tectorum* L.) form the simple communities with which this study is concerned. These annuals, all alien species, are weeds indirectly fostered by agricultural activities and in southcentral Idaho they are the first to cover the ground where sagebrush (*Artemisia tridentata* Nutt.) and its associated native perennials have been removed, especially on abandoned farm lands. The description of the communities, the order in which they appear, their extent, their relationships to man's activities and to pertinent native animals have been dealt with previously (Piemeisel 1932, 1938, 1945; Piemeisel and Chamberlin 1936).

THE GENERAL CONDITIONS UNDER WHICH THE COMMUNITIES THRIVE

The constituent species of the three communities have a widespread distribution that extends into humid regions and as scattered individuals or in small groups can live under a wide variety of conditions. However, extensive communities formed by these species are limited to the dry regions of Western United States and of these, the semi-desert region is the only one in which the three communities are the principal ones on denuded lands. Extensive areas of one or two may occur in the semi-arid regions, i.e., the Great Plains, but the communities that cover cleared lands also include those formed by other species and the plant cover is more complex. In the semi-desert region, and more specifically, within the general area originally covered by the sagebrush-grass type of vegetation, all three communities are common on cleared lands if they are near to cultivated tracts. Denuded areas remote from cultivated lands may sometimes be covered with native annuals. Other vegetation types of the semi-desert region, such as greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) and saltgrass (*Distichlis spicata* (L.) Greene) are closely associ-

[1] The writer is indebted to Dr. Eubanks Carsner for painstaking work on the manuscript and for helpful suggestions in the progress of the investigations.

ated with soils that have a high soluble salt content and on cleared lands formerly covered by these types there are communities of other annuals, salt-tolerant weeds, such as smotherweed (*Bassia hyssopifolia* (Pall.) Kuntze). Cleared lands formerly covered by other types of vegetation such as mountain brush or mountain forest are shared with communities of other species. Roughly then, all three of these communities thrive under conditions represented by cleared lands near to agricultural tracts and formerly covered by sagebrush-grass.

Order of Appearance of the Communities

Since the constituent species are annuals with a new generation each year and the changes from one community to another are rapid, it was possible to observe the various changes and then subsequently to attempt to induce series of one kind or another by modifying the conditions. On open grazing lands the series of changes were not alike on a number of areas under observation but became alike when upsetting influences (destruction of vegetation by any cause) were minimized. This was done by excluding domestic animals and rabbits, and by preventing burning or plowing.

Wherever destruction of vegetation was relatively slight the communities arranged themselves in the following order: first, Russian-thistle; second, mustards; and third, downy chess. This is the potential order of appearance towards which the series of changes always tend wherever the three communities are the principal ones and, if not interrupted by excessive destruction of the plants, the changes from the first to the last stage were achieved in approximately the same length of time, five years, on various areas under observation. This span of time was approximately two years for the first or Russian-thistle stage, two years for the second, the mustard stage, and the third, the downy chess stage, from the fifth year on. This optimal space-time

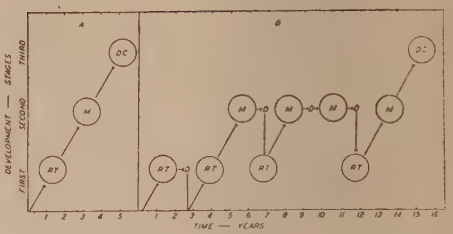

Fig. 1. Changes in vegetation from Russian-thistle (RT) to mustards (M) then to downy chess (DC). At the left (**A**) the straight line represents changes on all observed areas where destruction of vegetation was negligible. In **B** changes where destruction of vegetation indicated by D, occurred at varying intervals. This irregular line represents only one of many observed variations.

order of the communities, which is a potentiality on open grazing lands, becomes an actuality which can be observed and measured when destruction of vegetation is sufficiently reduced.

The potential order which is realized under controlled conditions can be represented diagrammatically by a straight line as in figure 1**A**. This represents any one or all the areas observed under controlled conditions. The irregular line in figure 1**B** illustrates only one of the areas where excessive destruction of vegetation occurred. If all of the areas under observation on the open-grazing lands were represented there would be a variety of irregular lines depending on the time when excessive destruction occurred. The outcome under the conditions of **A** (fig. 1), where there is control, is predictable. Under the conditions of **B**, where destruction may occur at one time or another, such as on the open grazing lands, the outcome is not predictable for any given area. It would be necessary to have foreknowledge of both the kind and amount of destruction and also the place in the series when it occurs. Whenever there is destruction there is a setback and if it is excessive there is a return to a previous status or to bare soil. If destruction is moderate, though still sufficient to destroy most of the com-

ponents of the succeeding stages, then the species currently dominant continues as a dominant the following year. Only when destruction is negligible is there assurance of development at the optimal rate.

In figure 2 the diagrammatic illustration of changes from one community to another is limited to conditions where

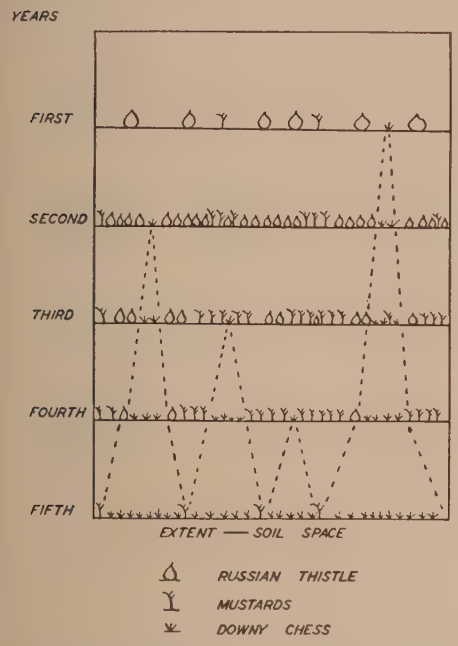

FIG. 2. Diagrammatic illustration of changes from one community to another under optimum conditions for development. Beginning with a Russian-thistle stage at the top and ending with a downy chess stage in five successive years and on the same soil area. The increase in area covered by downy chess is emphasized by the dotted lines.

there is an optimum or near-optimum for the spreading of each species and destruction from any cause is at a minimum. The large, widely-spaced Russian-thistle individuals of the first year (at the top) are followed by a dense stand of small plants the second year. This quick increase in occupancy of the soil space in the second year is temporary and is followed by lessened occupancy by Russian-thistle the third year. And here in the third year is an important period in the timing since, if some of the area is not to remain bare, mustards must have been increasing in numbers up to this time so as to take over the ground relinquished by Russian-thistle. The same timing must take place in the fifth year if some of the area is not to remain bare and downy chess must have been developing in the preceding years so as to take over the ground after the mustards.

At any stage, aside from the current dominant which covers a major part, part of the area will be covered by the succeeding dominant and commonly, a small part of a remnant of the preceding stage. At the end of the fifth year a major part of the area will be covered by downy chess and a part by the remnants of mustards. Russian-thistle if present in some small islands the fifth year is subsequently rare or lacking altogether. Remnants of mustards persist in succeeding years around the burrows and trails of mice, chiefly meadow mice (*Microtus montanus nanus*) (Piemeisel 1945). Depredation by these is not of significance until after the downy chess stage is reached. For the present studies the elimination of mice seemed too much of an undertaking for any sizeable area or for anything but short intervals and in no case sufficiently long to demonstrate that, without the mice, mustards too become rare or are entirely lacking. Inference based on observations on various areas indicates that this will take place.

Destruction of a future dominant, a selective destruction, need not involve any great quantity of vegetable matter if it is at a critical time in the series. Thus, if the small representation of downy chess in the first years (fig. 2) were destroyed, the total quantity removed would be small. Where such removal occurs for several successive years, it prevents development of the downy chess stage correspondingly.

Development within the Community

Development within the community has a direct bearing on an understanding of the causes that make for changes from one community to another. Such development is best observed in the downy chess community and the discussion here is largely concerned with downy chess.

The development of the downy chess community from one or a few individuals, then to clusters, and finally to dense patches, has already been indicated in figure 2 and was observed first in Field 4 (Piemeisel 1938). At that time the term "patch" was used in the ordinary sense. Since Watt (1947) has used it in a different sense the term "island" is now used for the small areas of downy chess separated from any large body of it and surrounded by some other dominant, usually mustards. This development of an island from a few plants to a dense stand is diagrammatically illustrated in more detail in figure 3. The increase in density which takes place in four years here represents the development of an island somewhat removed from any main body of downy chess since small areas contiguous to established stands will be influenced by an influx of seed and the time of development correspondingly shortened, as discussed later.

The arrangement which was in time sequence in figure 3**A** is repeated in **B** in spatial sequence at a given time. It is a diagrammatic representation of a cross-section of a nearly circular area, a small island. Such islands, as small as a few feet in diameter, were frequent in parts of a field in 1941 where downy chess was beginning to establish itself. The zones in the island from the inner dense central disk to the outer scattered individuals were marked by differences in maturity of individuals, in height, in color and degree of head emergence. At the center is a disk (4) composed of a very dense, short growth of immature plants of bleached straw color, with barely emerging heads or if emerged then prematurely dried. Next, and surrounding the inner disk, is an intermediate zone (3) of sparser growth where the plants are taller, of a deep purple color, and fully headed. Then an outer fringe (2) of very sparse, very tall green plants also in head. Finally, beyond the outer fringe are scattered individuals, solitaires, (1) green, well-stooled plants, not yet headed, and, situated in a surrounding stand of mustards. In the inner disk there was not a natural heightening of color preceding maturity, a change from green to purple and to a rich straw color, but instead, merely a fading of color from a green to a grayish green and then directly to the pale straw color.

Fig. 3. Development of a downy chess island. **A**—Time sequence covering four seasons on the same soil area beginning at the top (1) with a single tall plant and ending with a dense, short stand (4). **B**—Complete development from 1 to 4 as in **A** but here in spatial sequence at the same date. The dense stand in 4 is prematurely dry and the single plant in 1 has not yet headed. Characteristics of groups 1 to 4 are given in table I.

These sub-groups or age-groups of an island are developing parts of the downy chess community. The following terms for the four sub-groups have been adapted from Watt's studies (1947): "Beginning" for the first, the outermost zone; "young" for the second; "mature" for the third; and "degenerate" for the fourth, the innermost disk. The characteristics of the four sub-groups are summarized in table I.

TABLE I. *Characteristics of the sub-groups of a community of Downy chess*

Designations	Sub-groups or age-groups			
Numerical	1	2	3	4
Descriptive	Beginning	Young	Mature	Degenerate
Density Descriptive	Solitaire	Sparse	Dense	Very dense
Density Numbers per $\frac{1}{16}$ sq. m.	1 to 5	5 to 25	25 to 200	200 to 500 or more
Space per plant sq. cm.	125 to 625	25 to 125	3 to 25	1 to 3

The solitaires, though sometimes more than one per sample ($\frac{1}{16}$ sq m), have sufficient soil space so that their growth is near the optimum for the conditions of soil and weather. They are surrounded by individuals of other dominants, usually mustards. At the other extreme of development, downy chess may be the sole species, the individuals extremely crowded and depauperate. Their numbers within a $\frac{1}{16}$ sq m sample may reach 500, sometimes more. Stewart and Hull (1949) list up to 1,400 per sq ft, about 943 for a $\frac{1}{16}$ sq m. Usually in the areas studied and on the sites formerly covered by sagebrush and grass, the number was under 500 per $\frac{1}{16}$ sq m.

The spread and development of downy chess are evident from a 20-acre abandoned, cleared area where 182 fixed sampling points were located and where records were kept on the same unit area ($\frac{1}{16}$ sq m) at each of the points for a series of years. The time sequence is shown in 131 of these unit areas where the development of downy chess proceeded from one or a few plants at its first entry to 25 or more individuals. The samples containing downy chess are charted in figure 4, showing their distribution and the state of development in each, though all those samples with 25 or more individuals include both the mature and degenerate age sub-groups.

The spread of downy chess began from a roadside paralleling the top of each rectangle in figure 4. The manner of spreading can be likened to a grass fire which advances along a line or belt but which also throws sparks ahead of the line. Each spark then starts a separate area of fire sometimes at some distance ahead of the main belt of fire. These small isolated areas are comparable to the islands of downy chess.

The beginning age is represented by the largest number of sample areas in the fourth year of the series (fig. 4) and the young, in the fifth year. The mature and degenerate ages appear at the top first, become numerous there in the fourth year and prevail over the entire area in the sixth year. However, if based on percentages of samples that contain downy chess in any one year, the beginning age has the highest percentage in the first year, somewhat less the second,

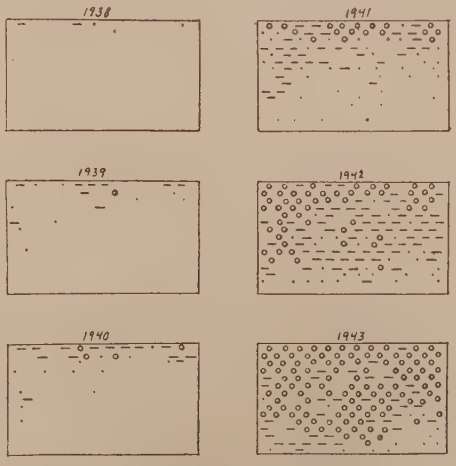

FIG. 4. Successive charts of a 20-acre field where there were 182 fixed sampling points and where records were kept on the same area ($\frac{1}{16}$ sq m) at each of the points for a series of years. A sample containing downy chess is indicated by a symbol showing the age or maturity of the stand: "Beginning" by a dot; "young" by a dash; and a circle indicates both "mature" and "degenerate" ages. Lower edges of the figures face north. Prevailing winds are westerly (from right).

third, and fourth, after which there is a rapid decline. The young age shows highest percentages in the third and fourth years, and the mature and degenerate ages, by far the highest in the sixth year.

If the 131 samples in which time sequence is shown are arranged according to the first year of entry of downy chess into a sample, the largest number (43%) fall into a group with a 2-year increase, beginning with an average of 7 individuals and then 25 or more the second year. Nearly as many samples (39%) showed a 3-year increase beginning with an average of 4 individuals, then 12, then 25 or more. About 10 per cent had a four-year increase with an average of 2 individuals the first year, 5 the next, then 11, and finally 25 or more the fourth year. The longer rates of 5 and 6-year increases involved few samples (4% and less than 1%, respectively). The other extreme, with a one-year increase with 25 or more plants at the first year of entry, also involved few samples (4%). The yearly increments may or may not represent a distinct age group as for instance the 6 and 11 individuals of the 4-year increase would both be of the young age group. Also, since the final year of these rates contains 25 or more individuals, it represents both the mature and degenerate ages so that for those merely mature one year more at least would be needed to reach a degenerate age.

The rate of increase within the sample areas is dependent on the position of the particular sample area with respect to established areas of downy chess. Thus any sample area next to a stand of downy chess would show a rapid increase in density because of the added influx of seed and at the first entry within the sample the numbers would be comparatively high. However, there would be few so situated at the beginning of the series of changes and comparatively many towards the end. A sample representing an island some distance removed from the main body or established stand would show a slow rate of increase whether in the early or late part of the series, though there would be comparatively few so distant towards the end of the series.

The cover of downy chess for the field as a whole then consists of varying densities which represent different ages of maturity of the community. The field grazed or burned may show a higher degree of uniformity in age because of thinning. One of the most uniform stands observed was on such a field. The beginning and young ages composed the cover of the field whereas the degenerate was lacking and the mature was rare. But very heavy thinning and especially if accompanied by a disturbance of soil results in a readmittance of mustards or Russian-thistle and the changes from one community to another set in. Barring disturbance of vegetation the parts of the downy chess cover that reach the old or degenerate age again revert to a beginning or young age and there is a repetition of development through the successive ages of the community. It is a cyclic change which involves only successive ages of the same community and contrasts with the sub-seral changes from Russian-thistle through mustards to downy chess. Russian-thistle and mustards do not have the same opportunity as downy chess to go through this sort of cyclic change since the next succeeding dominant cuts in on the cycle. Downy chess may also be cut short in its cyclic changes if native perennial grasses are sufficiently abundant to take over the ground. It is true that either Russian-thistle or mustards may continue to dominate a given area where disturbance of vegetation is such as to kill out the succeeding dominant but this continued dominance is not the result of cyclic changes since these as well as the sub-seral changes are disrupted by too great disturbance.

The cyclic changes and the development within the community as described above have some features in common with those described by Watt (1947) though his

studies dealt with complex communities of perennials and with changes which as he states some authors regard as seral. The term "phases" which he applies to sub-groups of the communities he dealt with would also seem to apply to the sub-groups or age-groups of the downy chess community but use of the term phase is left until the processes within a community are much better understood. His term "patch" he regards as synonymous with "phase." The term island used for downy chess represents an entire small community.

The downy chess community consists of individuals all of which are of the same generation and of the same age measured in units of time but in the sub-groups the individuals are of different age (physiological age) in terms of maturity, degree of development as measured by head emergence. This is seen at its best in the spatial arrangement of a well-developed island where all individuals are of the same generation and of the same age (time) but those in (4) the degenerate sub-group or age-group of the community are of different maturity (head emergence) from those in (3) and (2). A downy chess community is complete when it includes all of the sub-groups. In a community under severe disturbance as the one mentioned in the preceding paragraph, the earlier age-groups form a disproportionate part of the community.

As previously stated, the studies of Russian-thistle and mustard communities have not been followed as well as those of downy chess. To do this it will be necessary to keep the next succeeding dominant from developing in the area under observation and so prevent a disrupting of the cycle. It will be necessary to do this in such a way as not to disturb the communities being studied. Communities of Russian-thistle and mustards mature and degenerate much more quickly than downy chess. Observations on this are many but not on the complete cyclic changes.

In the study of development in plot 4 (Piemeisel 1938) the statement was made "this increase in number of individuals per unit area was not a gradual one but rose to peaks at irregular intervals." For the series as a whole the peaks occurred for each dominant and also the numbers were progressively higher for each successive dominant. The rise in numbers to a peak of density is evident in the individual downy chess island. It is evident in the numbers of downy chess plants in individual samples for successive years or in the average of large numbers of such samples. It is evident also in the frequency data for each successive dominant. Watt (1947) suggests "that a curve of the growth or logistic type expresses the general course of change." His reference is to total production of vegetable matter. With annuals statistical studies can be based on the number of individuals since, in spite of the defects of the method, it could serve as a good beginning.

Frequency curves based on the percentages of 182 samples ($\frac{1}{16}$ sq m) for a 20-acre field are presented in figure 5.

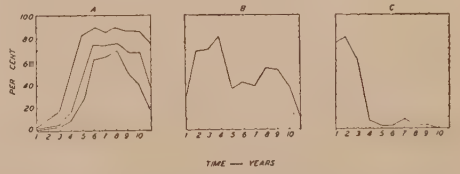

FIG. 5. Frequency curves for an 11-year period 1938–1948 based on the percentages of 182 samples in a 20-acre area. **A**—Downy chess. Upper curve for 1 or more plants; middle, 10 or more; and lowest, 25 or more. **B**—Mustards. **C**—Russian-thistle.

In **A** the three curves represent different densities (1, 10, 25 or more plants, respectively) of downy chess for an 11-year period. The general trend is much the same in all three but the decline is most marked with a density of at least 25 plants (innermost curve). This decline took place in the presence of a corresponding increase in native perennial grasses. The slow rate of increase for downy chess

(fig. 5**A**) in the first years is evident.

In figure 5**B**, the increase and then decline of mustards represent the same field and same number of samples as in **A**. A rapid decline of Russian-thistle is represented in figure 5**C** also for the same field and the same number of samples. The initial increase of Russian-thistle not shown here is extremely rapid as compared to downy chess.

It seems that the rise and decline in each of these communities can be expressed by the growth type of curve and that these communities of annuals would readily lend themselves to statistical studies that would bring this out clearly.

Why One Community Gives Way to Another

Why one community gives way to another is an old question. It is here applied to a particular kind of vegetation and furthermore to the optimal space-time order of arrangement of the communities as discussed above under the heading "Order of Appearance" and shown in figure 1**A**. The question here does not include the many variations that are possible where destruction of vegetation takes place as in figure 1**B**. Thus, it is understood that the plants remain intact and also that there is a reasonably good and uniform soil. With these limits set for the inquiry there is more hope of making progress toward the answer of the general question.

The information, on which parts of this section are based, has been previously published as will be indicated later. The intervening years have given time for further consideration of the earlier conclusions and for more experience in the field with regard to them. Thus further analysis of the many causes has led to the attempt at a more inclusive synthesis in answer to the question of why one community gives way to another.

Of the influences that affect these communities there are two kinds: (1) widespread, external influences such as precipitation, that also affect large areas alike if they are flat or nearly so, and (2) local influences, external or internal, that may involve spaces as small as a few square feet. Local influences such as abrupt and obvious changes in soil or slope can be avoided in the selection of an area for observation. Local influences such as direct destruction of vegetation can be prevented sufficiently for the series of changes to take place and are not being considered here as mentioned previously. Local effects arising from the characteristics of the plant species or their communities (internal influences) are considered later. The main concern for the moment is with the first, the conditions that are widespread.

Climatic conditions, as indicated by the sagebrush-grass type of vegetation, are characterized by a low precipitation (about 10 inches) and by dry summers. These conditions have had a profound effect by eliminating many species not suitable to this region and to this extent have determined the species that compose the communities. Of the species that can endure the conditions, some are represented only by scattered individuals but not by any sizeable communities. Thus not only the species but also communities of these are limited to the few that can meet the requirements of low total precipitation and the dry summers. Here is a background for all of the following discussion that is easily forgotten when attention is for the moment centered on a single factor. It is: these communities can thrive and reproduce themselves under the conditions of low precipitation and the dry summers.

In the sagebrush-grass type of vegetation the physical factor most commonly at a minimum is water. Only the top layers of soil are wetted by the current season's rains and the lower layers are perennially dry. The soil mass on which the plant can draw for its water is therefore limited in depth and for a given soil this is roughly proportional to precipitation. Also, since the individual plant rarely grows by itself, beyond the reach

of the roots of other plants, the soil mass is limited laterally as well as in depth and this lateral extent is determined by how closely the plants are spaced. If the number of individuals on a unit area is high there is crowding with a resulting restricted soil mass upon which the individual plant can draw for its water.

The soil moisture accessible to an individual plant of these species in any given season is affected: (1) by precipitation (the total amount of water put into the soil); (2) by spacing or density (how a given quantity of water in the soil is to be shared by the individuals). An

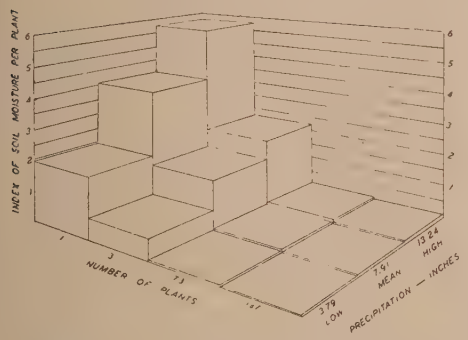

FIG. 6. The comparative amount of soil moisture available for an individual plant based on precipitation and the number of plants per 1/16 sq m. The tallest column in the background indicates the highest amount, that available for a lone plant with the highest precipitation. In the foreground the low amounts are for the individual plant of a dense stand. At the extreme left is the comparatively high amount for a lone plant with the lowest precipitation on record.

attempt is made to illustrate this relationship in figure 6. The basis for it is the previously published data for a permanent square meter quadrat from Plot 4 near Hollister, Idaho (Piemeisel 1938). This quadrat is chosen because it escaped any noticeable destruction throughout the five years. The number of plants was originally given for one square meter but since in this illustration a single plant uncrowded by others is also being considered, a unit (1/16 sq m) is chosen because a single plant of the species involved can scarcely fully occupy a square meter with its roots. Thus all the numbers have been divided by 16 which gives 3 for the lowest number in the series, 73 for the mean, and 147 for the highest. Precipitation from a 30-year record for Hollister, Idaho (U. S. Weather Bureau data 1913–1942) gives the lowest for the record as 3.79 inches; the mean annual as 9.31 inches; and the highest as 13.24 inches.

The greatest amount of water that an individual plant can get is that under the highest precipitation and where the plant is by itself, the water not shared by others—shown as the tallest column in the background in figure 6. The second highest (next column left) is a lone plant with mean annual precipitation, and the third (column at the extreme left) is a lone plant with the lowest precipitation of record. These are all comparatively high values but there is a rapid decline to the right as the number of plants increases from three to 73 and then to 147. In the latter (extreme right) where the plants are crowded, the values must be exaggerated to show them on this scale and the total amount for the individual plant is extremely meager no matter whether precipitation is high or low. The figure illustrates how well a lone plant, not crowded by others, fares under the lowest precipitation and how precarious the situation is if the number of plants is high even though precipitation is at its highest. This is the essential point in the illustration.

The method of illustrating the water relationship seems essentially sound even if the representation cannot be defended in all particulars. Aside from details, it is supported by these two general and verifiable points. The variation in precipitation is comparatively slight. The lowest recorded is commonly doubled but rarely trebled and a 4-fold to 5-fold increase has not been recorded. The increase in numbers of plants per unit area for the series of years is comparatively great. A better than 10-fold increase is

to be expected, a 50-fold increase is common (roughly equal to that of plot 4) and a 200- to 300-fold increase is frequent. In the beginning of the development from an initial stage to a downy chess cover the number of plants per $\frac{1}{16}$ sq m may be often as low as one. At the end of the 5-year period it is frequently as high as 300 or more per $\frac{1}{16}$ sq m. Viewed in this light the illustration is conservative. In the field some small, dense areas dry prematurely in a year not in any sense a drought year, as in 1941 when the Sept.–June precipitation was approximately 10 per cent above the mean. Also, sparse stands have survived in the severest drought year on record.

Up to this point discussion of figure 6 has been concerned with the total number of individuals without distinction as to species or communities. However, in the changes from the first to the third stage there are involved stands of three successively dominant species. Some comparison of the three kinds of communities can be made by seeing to what extent each can be crowded, that is the point at which seed is not produced and there is failure as to continuance of the dominance the following year. By using the method of figure 6 and by taking again the records of Plot 4, the comparative points at which the dominants fail to produce seed is represented in figure 7. The number of plants per $\frac{1}{16}$ sq m for Russian-thistle

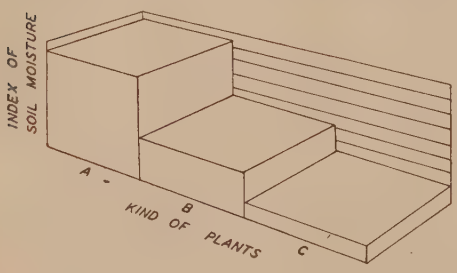

FIG. 7. The comparative amounts of soil moisture available per plant as indicated by the heights of the three columns: extreme left (**A**), when Russian-thistle failed to produce seed; middle (**B**), when mustards failed; and right (**C**), when downy chess failed.

when it failed to produce seed was 43 and precipitation was 89 per cent of the mean seasonal (Sept.–June); for mustards 63, with precipitation at 64 per cent; but downy chess managed to produce seed and continue its dominance when the numbers were 113 and with precipitation at 53 per cent. A figure obtained from another field for the failure of downy chess gives 290 individuals with precipitation 91 per cent of the mean seasonal.

If the column at the left, figure 7**A**, is drawn to represent the amount of water available for an individual of Russian-thistle when it failed to produce seed, then on the same scale (space per plant × percentage of mean seasonal precipitation) **B**, the middle column, is the proportionate amount for an individual mustard when it failed and died prematurely, and the column **C**, when downy chess failed. Conditions would need to be better than in **A**, **B**, or **C** for any of these to produce seed. In pure stands then, Russian-thistle reaches its peak of density when the numbers are comparatively low and downy chess when the highest. Mustards take an intermediate position. Roughly, downy chess can survive with approximately half the amount of water per plant as compared to mustards and $\frac{1}{5}$ that of Russian-thistle.

In the pure stands of any one of the dominants just considered, the individuals all make their greatest demands for water at approximately the same time. It is an important point since, with a strictly limited soil moisture supply, it would be a great advantage if the individuals of any one of the dominants drew heavily on the soil moisture before those of others. Thus in the areas where communities of the dominants meet and mix, the time of growth of each of the species becomes an important consideration and especially so in its relation to the time of greatest abundance of soil moisture.

In figure 8**A** are given the average percentages for soil moisture in Plot 4 for the period 1928–1932 for a depth of 0–36 inches. For the present purpose and

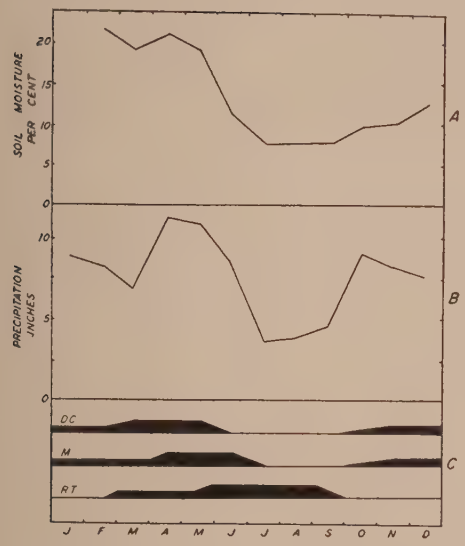

FIG. 8. Seasonal trends in (**A**) soil moisture; (**B**) precipitation; and (**C**) periods of growth for the three dominants: DC = Downy chess, M = Mustard, RT = Russian-thistle. In **C** the highest part of the shaded horizontal bars indicates maximum growth activity; the lower, slight activity; and the narrow line, none, i.e., when the plants are dead and the species are being carried over by seed. The breadth of the bars, left to right indicates the time of year covered. (Note: The precipitation scale should read 0.5 and 1.0 inches.)

since the same soil area is represented throughout, the values for total moisture content are used and stated as percentages of dry weight. Soil moisture is at its lowest during July and August and highest from fall to spring. The general trend is similar to that of precipitation in figure 8**B**, where monthly means are plotted for Hollister, Idaho (U. S. Weather Bureau data 1945).

The time of growth (its beginning, end, and greatest amount) is represented in figure 8**C**, for each of the three species of annuals. Growth of downy chess (DC) begins in the fall (at right) as soon as rainfall becomes sufficient; is halted by the coldest weather; makes the greatest growth in early spring (left middle) and matures before the hot dry weather sets in. Mustards (M) also begin growth in fall but differ in making their greatest growth and in maturing somewhat later. But Russian-thistle (RT), unlike both, begins growth in spring; is still in the seedling stage when the other annuals have made their greatest growth; makes its greatest growth in the hottest and driest time of the year; and matures about the time of frost in fall. Downy chess and mustards begin to draw on the soil moisture in fall and make greatest demand for water in spring at the time of their greatest growth and when soil moisture is most abundant; whereas, Russian-thistle calls for most of its water in hot weather when the other two are already mature, when rains are rare, and when soil moisture is at its lowest.

Individual plants are affected then (in the amount of water each will get) by the crowding of individuals of its own kind which draw on the soil moisture at the same time in pure stands but in mixed stands are also affected by individuals of other species which by their earlier growth may exhaust or greatly reduce the limited moisture supply.

Up to this point soil moisture, in its quantity and in the way it is shared, has been considered with respect to the effect on individuals of groups and also on their respective groups during a single season and a single generation of plants. The effect resulting from both a low initial water supply and from crowding does not end with the generation but also affects the next generation and other influences, plant characteristics, such as seed production, become important. Crowding is dependent on seed production of the preceding year. Crowding in pure patches of the dominant means heavy seed production of its own kind in the preceding year. In mixed stands the crowding of the outgoing dominant is affected also by the preceding year's seed production of the incoming dominant. But the capacity to withstand crowding varies with the dominants as previously discussed with figure 7. In the second year there is crowding for Russian-thistle

but not for mustards or downy chess. Crowding then can be discussed only if a given group or community is kept in mind and if it is related to the general process that is taking place—as to what has happened in the preceding year and what will happen in the succeeding year. Seed production and seed distribution are both affected by the degree of crowding and must be discussed with regard to a particular dominant and in relation to the general process. Thus Russian-thistle in the first year has an opportunity to produce a large quantity of seed on the large plants and these rounded plants are broken off by the wind so that a good scattering of seed is possible. But in the subsequent dense stand the slender, closely-spaced plants remain in place and the comparatively few seeds fall nearby.

All of these processes are interwoven, affect one another, and since a discussion of these one at a time is unsatisfactory, an attempt is made to present all of the principal ones for consideration at the same time by means of a series of polygonal graphs after the method of Hutchinson (1936) to illustrate the part that each group or community takes in the series of changes.

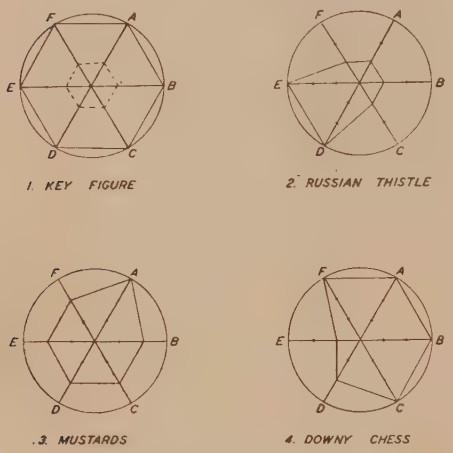

FIG. 9. Comparison of the values of plant characteristics for gaining control of the ground and for holding the ground once gained. Arrangement of values is from the center (zero) outward, as low, medium, and high. Maximum values are shown in the key figure (upper left) at the circumference and minimum values are indicated by dotted lines. A = priority in germination; B = earliness of maturity; C = capacity to withstand crowding; D = seed production; E = seed distribution; F = earliness of maximum growth.

The top left, No. 1 in figure 9, represents a situation where all characteristics are at an optimum and where the values from zero to low, medium and high are arranged from the center outward to the circumference. This key figure affords a standard against which the various dominants can be compared and is an ideal, since theoretically any one of the dominant annuals which possessed all of the characteristics at their fullest value would occupy an area the first year and hold it against the others thereafter. Conversely, the space within the broken lines, No. 1 in figure 9, represents the minimum values, an unsuccessful annual, though of this kind there are actual representatives.

The three types represented by Nos. 2, 3 and 4 in figure 9, illustrate the comparative differences in the characteristics of the three communities and help to understand why one of these occupies the ground first and then yields it to another. Russian-thistle (No. 2 in fig. 9) rates high in seed production and in seed distribution which indicates why it can cover the unoccupied ground quickly, and therefore takes first place in the series. It is low in other qualifications which go toward holding the ground once it is occupied. In these it approaches the unsuccessful plant. Mustards (No. 3 in fig. 9) exceed Russian-thistle in time of germination, earliness of maturity, capacity to withstand crowding, and consequently Russian-thistle yields the ground to them. In the second year of occupation when Russian-thistle is dense and dies prematurely the less numerous but large individuals of mustards thrive, produce an abundance of seed and seed the ground heavily for the following year. The mustards by their growth precede the crowded conditions of Russian-thistle and so es-

cape the effects of the crowding. Downy chess (No. 4 in fig. 9) exceeds both mustards and Russian-thistle in those characteristics which tend to hold the ground. It is weak in distributing its seed quickly in large quantities at any distance and hence is comparatively slow in its progress of covering a given area. But just as mustards escape the crowded conditions of Russian-thistle so downy chess in dense stands of mustards produces seed also by escaping the crowded conditions through its earlier maximum growth and earlier maturity.

Of the three annuals, downy chess approaches the pattern of No. 1 (fig. 9) more nearly than the others and Russian-thistle the least. In contrast the sunflower can be represented by the part limited by the broken lines of No. 1 (fig. 9) and as an unsuccessful annual on cleared sagebrush-grass lands. It rarely occurs over any sizeable area and then only as scattered individuals uncrowded by other plants. However, it is a common weed on unoccupied waste irrigated lands or on newly disturbed soil along roadsides and is also a weed on abandoned lands in the higher valleys of foothills and mountains.

Each of Nos. 2, 3, and 4 (fig. 9) represents a group of individuals and at a time when the group is attaining its maturity. Later, in the degenerate age of the group, when crowding has reached the limit of the capacity for the group, the polygonal shape shrinks to that of the unsuccessful annual of No. 1 (fig. 9). Seed production and seed distribution become at their minimum and other characteristics are rendered ineffective by the premature drying.

Why Certain Conditions Bring About Uniformity in Rate of Change

That there is uniformity in rate of change has been discussed elsewhere (Piemeisel 1945). Here the question is, why it occurs.

The following discussion concerns the vegetation of annuals on cleared sagebrush lands in southern Idaho. The same rate of change may or may not apply to a vegetation of annuals elsewhere. It is a question for future studies to determine whether there is a potential rate of change for each set of communities of annuals for a given climate and soil, and whether this potential is always realized if, locally, certain conditions are fulfilled. Also, what should be obvious but what is easily overlooked, is that the following discussion cannot be applied directly in a comparison with the open grazing lands where the whole complex of factors is at work currently and has been for years in the past. Nor can the statements be applied directly to so-called "protected areas" where livestock alone is removed and destruction by other animals is disregarded.

Since the discussion here concerns a potential, the conditions under which this is to be realized must be specified and the area on which it is to be observed must fulfill the conditions. The selected area should be one where there are no obvious or abrupt changes in soil; where the soil is not actively drifting; where, at the beginning of observations, the species involved in the changes are each represented by some individuals; and also, where direct destruction of the stands of each species is prevented. On areas fulfilling these conditions there is a uniformity in rate of change in cover; that is, downy chess covers a major part of each area in approximately five years. With present knowledge the time is five years in terms of the dominant over a large part of the area. It includes all soil space within the area wherever downy chess is the dominant species whether the stand is sparse or dense. The time is more nearly 6 years in terms of a mature downy chess community over a large part of the area, a dense stand over most of it. With better measurements the time may be more closely fixed or the end result more precisely stated but the concern here is less with the precise time and more with the

question as to uniformity in rate under certain conditions.

On newly abandoned lands part of the seed supply is already on the ground and part comes from the old fence rows, roadsides, ditches, etc. On these lands there is the best opportunity for the study of rate of change. Seed of the three successive dominants is usually present from previous farming activities. There is considerable variation in the proportions of the three dominants in the stands of the first year. On a bare, plowed and abandoned field, the first year's stand may be extremely sparse but as a result the Russian-thistle plants are large and heavy with seed and much of the disadvantage of the small number of the first year is overcome by the second. In extreme cases, if mustards greatly outnumber Russian-thistle, then the first stage is less well-developed and less clearly marked the second year. However, any gain is lost at the mustard stage unless downy chess has also increased proportionately which is unlikely except as noted in the next paragraph. Obviously on old abandoned lands if downy chess is better established in the first year of observation the time for downy chess to cover the area will be less.

Size of the area is of principal concern in rate of change if the seed or most of it is to come from the border. As stated previously, on newly abandoned lands seeds of these species are present from the crops grown before abandonment. Moreover, though cleared abandoned lands have been found miles in extent, these were sub-divided by old roads, old ditches, fence rows, or drainage channels that harbor these weeds so that the area, if it is to be seeded from the borders, is more nearly 40 acres or less. Variations in area within this medium-size class seemed to have no noticeable effect on the rate of change. However, if small or very narrow areas are surrounded by stands of downy chess, then the rate may be greatly accelerated because of heavy seeding from the borders and the time reduced to one half or even less (Piemeisel 1945). This is seen, too, in the sample areas as discussed in connection with development within the community.

Since on a large area as a whole, a wet year (above average precipitation) is commonly taken to mean an increased total amount of plant growth, and a dry year (below average precipitation) a decreased growth, it is natural to assume that this would necessarily result in a corresponding increase or decrease in the rate of change on a particular area. However, this is not borne out by observations on selected areas nor does it seem to be so from an analysis of the processes as they are understood at present. In a dry year the effect of the crowding is accentuated. It is, however, the stage that is outgoing that is for the most part crowded. The dry year then has its greatest effect on a stage that is in any case going out and it merely goes out more completely. The incoming stage represented mainly by uncrowded plants is not affected sufficiently to prevent seeding and consequently there is further spreading next year. The net result of a severely dry year then is not to hasten the change but to make the transition from one stage to the next more distinct. While this results in an additional area that is covered solely but sparsely by the incoming stage in the following year, it does not affect the rate at which this incoming stage develops.

In a wet year the increased moisture results in a larger vegetative growth for equivalent stands but this does not mean a greatly increased seed production for the crowded stands of the outgoing stage. It does not relieve the crowded conditions and if there is increased vegetative growth, a greater amount of soil moisture is required and it is used at a faster rate. Even assuming that a somewhat greater amount of seed is produced for the outgoing stage it is necessary to consider both the incoming stage and the development the next year to see if the rate is affected. Seed production of the widely

spaced plants of the incoming stage may be increased but if so it can only accentuate the expected crowding of the following year. In such a crowded stand the possible effect of some increase in seed for the outgoing stage just mentioned will be lost. Summing up, a dry year accentuates the effect of crowding in the current stands but principally in those of the outgoing stage. A wet year if it results in heavier seed production in either the incoming or outgoing stages accentuates the crowding in the subsequent year. The effect of either a dry or wet year is temporary; does not carry through the next stage and does not significantly affect the rate.

After seeing the changes take place in many areas and in different series of years with their different weather conditions, the conclusion is that under the specified conditions the rate of change is not determined by precipitation or by other meteorological factors but is governed by internal influences, the characteristics discussed in connection with figure 9. We come back to the statement made earlier—that these communities thrive and reproduce themselves within the vagaries of weather. On open grazing lands the greatest threat to their existence is destruction from a source external to the plant communities. With this eliminated it is possible to observe the effects of one plant community on another. Russian-thistle, mustards, and downy chess each spread at their particular rate and much as if the preceding stage were not there. This is of course literally true of Russian-thistle since it spreads over unoccupied ground, and nearly as true for mustards since they spread into former Russian-thistle areas and start to grow in fall when Russian-thistle is represented not by living plants but only by dried plants and seed. The two do not enter into competition until the following spring and by that time the mustards are well-grown whereas Russian-thistle must establish itself as a seedling, a very unequal competition. Russian-thistle then does not continue to occupy the ground after the second year chiefly because of the crowding of individuals of its own kind and a resulting lack of seed. But of the seed that is produced, the resulting seedlings if they occur mixed in a fair stand of mustards, do not mature. The inter-species competition is only part of the process and in some years a small part because of the great reduction of Russian-thistle through intra-species competition the preceding year.

The seed of downy chess enters former mustard stands and starts growth with mustards at that place at the same time. But downy chess grows more rapidly, overtops the mustards and matures earlier. This is more of an equal competition but here too inter-species competition may not occur to any extent the fifth year if in the preceding year no seed of mustard was produced as in Field 4 (Piemeisel 1938). In that case there was no inter-species competition the fifth year of the series largely because of the intra-species competition of the preceding year. The check on the continued dominance of each of the successive dominants is due first, to intra-species competition and next to inter-species competition. The first starts the checks and if not complete, the second completes it. Stated another way, the structure of one community weakens after maturity in the degenerate age, and leaves the ground poorly occupied and accessible to another. Alongside of this is the competition where communities overlap and the individuals of the outgoing community compete unsuccessfully with those of the incoming. The community first on the ground is there because of its rapid migration and development and the second, because of its greater capacity to hold the ground once it gets there.

What has been said about rate of change for communities of annuals also applies in general to those native perennials that next succeed downy chess as now understood from unpublished mate-

rial. What modification may need to be made is not yet evident. Advances in our knowledge of rate of change will come when studies are carried on under conditions where the constituent species can each spread without external interference. The study of the effect of each factor that interferes with the rate and the total effect of all such interference will naturally follow.

Some General Questions Related to These Studies

The foregoing pages open a way for detailed investigations concerning competition in successive generations of plants and in regard to development within the community. The essential conditions necessary for such investigations are present: the simple communities consist of one or a few species; the components have a short life-span which results in a quick turn-over, a rapid change from one community to another; and also the possibility of simplifying the conditions external to the communities by artificial means (by fencing etc.) so that each species may increase very nearly according to its capacity. Gause (1934) in discussing ecological succession among animals has already stated some of these as necessary conditions: "that an analysis must be made of comparatively simple desert or Arctic communities where the number of components is small" and also that "an active intervention into natural conditions by means of biotic experiments may also be very important." Here the intervention would include protection of the stands from destruction by any cause, even the damage by mice and not only for a short time but for several years if successive generations of the dominants are to be studied in detail. It would also include the manipulation of densities for comparative studies during the same season—for the same intensities of the meteorological factors. For complete studies of development within a community it would mean keeping out the next competing dominant which otherwise cuts short the cycle of development.

Investigations dealing with communities of annuals are all the more pertinent since up to the present time the investigations are largely confined to communities of perennials even if in some regions our vegetation over increasingly large acreages is being reduced to one of annuals and even though communities of annuals are commonly more accessible for such studies. This preoccupation with studies concerned with long-lived plants persists although it is obvious that underlying principles involving successive generations can be gotten at more readily where there is a quick turn-over of generations. The outstanding example of the use made of Drosophila for genetic studies has not made plant ecologists aware of the possibilities inherent in communities of annuals where the life-span is short and the changes rapid. A better knowledge of the processes that are involved in competition through successive generations of plants and of the development within a community is needed for practical application as well as to throw light on questions concerning the nature of communities and their changes. Some of these questions which are concerned in some respects with the discussions of the preceding pages are selected here for discussion because of their bearing on future investigations.

One question concerns drought. It is a useful term in agricultural activities for making comparisons between years of high and low precipitation and for approximately equivalent stands of plants, but is often of questionable value when taken over into ecological investigations. It is common to find drought ascribed as a cause where dying and drought are coincident and where no attempt is made to look further into the processes of change.

In an appraisal of the causes that brought about the premature drying of a small area there are two comparisons involved and usually implied. The first is

a comparison in time with an equivalent area of equal density which did not die in a previous year of average rainfall and where other factors have been ruled out, such as soil differences. Here drought is assigned as the cause. Next there is a comparison in space, made at the same date, between a prematurely dry area and a contiguous green one. Here, since soil conditions are assumed to be the same and the meteorological factors are of the same intensities for the two areas, the cause is sought in a difference in the arrangement or spacing of the individuals (a sociological factor) within the respective groups or stands of plants for the two areas. If both comparisons are intended or implied at the same time then both meteorological and sociological factors must be taken into consideration and together they determine the size of the area that is affected. In a drought year there is sufficient soil moisture to support individuals of the species—those in the adjoining sparse stand are evidence of this. It is the sociological factor in crowded groups which brings on a deficit that is lethal. If we can speak of a "physiological drought" in the presence of a sufficient supply of soil moisture then here we can say there is a "sociological drought." At least emphasis on this point is needed until it has received the attention it deserves.

Drought and premature drying can be considered as merely coincident until the various factors and processes have been examined. What has happened in the current year is pertinent but sometimes even more so what has happened in the past. A stand of perennials may have been so devitalized by grazing in the previous years that it would have died in a year of average precipitation. Drought is too easy an explanation of much of the premature drying. Once determinations have been made of the relation of extreme drought to a solitaire of the species, an individual not crowded by others; to age of individuals of the species and to the age of groups or sub-groups within a community, the whole question should be much better understood.

Another question is one concerning the effect of alien on native plant communities. A review by Wulff (1943) of articles dealing with one phase of the question indicates that there is little or no evidence that an alien plant community can survive in a native vegetation except with man's intervention. To say that some species fit in with man's activities and thrive whereas other species, including the native, cannot thrive because of such activities, is one thing. It is very different to say or to imply that the alien meets the native on the same soil area and through competition subdues the second. Statements to this effect are being made up to the present time and some date back at least to the time of Warming (1909) thus: "the hordes of European plants that have entered Argentine and have destroyed the indigenous vegetation here and there" and again: "American plants introduced into Europe have locally suppressed native species." The expressions "destroyed" and "suppressed" are misleading and Warming himself has a different understanding in another place when he states: "yet nearly all changes in vegetation that we see taking place—for instance, in forests in various parts of the earth—seem to be due to physical changes and particularly such as were caused by the destruction of forest by human agency." The discrepancy involves not merely expression or definition but different processes. These will not be clear until there are studies and demonstrations to show the particular role that the alien species play in the successions.

The results with the annuals indicate that the aggressiveness often attributed to alien weeds is largely limited to their entering a void in the native vegetation. Russian-thistle is aggressive in invading bare or poorly occupied ground and "replaces" the native species only in the sense that the latter have first been killed out by some external destructive cause.

Downy chess "supersedes" mustards (whether native or alien) by entering those communities, and then by its greater efficacy, holds the ground once it enters. These alien annual species may supersede without man's further intervention, either an alien or native dominant which plays a role which is antecedent to (or sometimes equivalent to) its own in the successions. However, the alien species do not generally come into contact with the native annuals. The two occupy respective areas that do not greatly overlap. In remote areas where the seed of the alien species has not been carried by man's activities, bare or poorly occupied soil is taken over by native species. These are adapted to take over comparatively small areas. It is man's activities that have greatly increased the size of the bare areas and though these activities are adverse to the growth of some species, they have incidentally selected other species that can survive and spread in spite of them. The alien annual species commonly invade bare spaces amongst the native perennials but do not invade such communities if direct destruction has not made way for them in the present or in the past. There is no known instance where these aliens, participants in the earlier stages of successions, supersede any native perennials except by man's direct or indirect interference. The question is not only whether the annuals can grow amongst the perennials in any one season but whether they can maintain themselves there. In areas of modified sagebrush-grass climax protected against rabbits as well as livestock but adjacent to areas of annuals there was eventually no penetration of annuals into the stand of perennials even with the opportunity of heavy influx of seed and during years favorable to the growth of annuals. The area was well occupied (except for eroded spots) by individuals of some of the principal species of the sagebrush-grass climax though many species were lacking and the original arrangement (spacing) was also lacking.

The degree to which either Russian-thistle or mustards can return to a site formerly occupied by them and currently occupied by downy chess is a question that concerns mustards principally, since Russian-thistle even with the damage done to the downy chess cover by mice, is very nearly eliminated from the area and only excessive destruction can bring it back as a dominant. But since mustards under these same conditions persist as an admixture in the downy chess cover they are ready at hand to take advantage of any unutilized opportunity and this is offered to some extent alternately in time on a given space. It also occurs in space in any one season in the sparse small areas that alternate with the dense. The areas covered sparsely by downy chess, subsequent to a dense stand, open a way for an admixture of mustards. However, it must be assumed that a considerable amount of seed has come in from an adjacent area of mustards. Also assuming that a scattered stand of mustard develops in the sparse downy chess, the mustards produce either a very small amount of seed or none except in very favorable seasons, depending on the density at a particular locality. And downy chess which is also present in some degree has the advantage the following year in the increased density and the resulting interspecies competition. Observations indicate that mustards would eventually be lacking because of a lack of seed. As it is, the breaks in the cover made by mice afford an opportunity for mustards to grow well, produce a good quantity of seed and the good-sized plants distribute it well whereas the plants growing with downy chess, if they produce seed, are small except in favorable years and the seed is shed around the parent plants. What needs to be known here is to what extent differences in densities persist after many islands of downy chess together form a cover over an area, and under conditions where damage by mice as well as by other causes is sufficiently reduced. With the last question the one concern-

ing the persistence of mustards is interwoven and could be dealt with at the same time.

In the questions considered above, plant-animal relationships are of primary importance and further advance in knowledge will result from a better understanding of these. With severe disturbance of vegetation or with partial protection after such disturbance there is an excessive reproduction not only by some species of plants but also of animals. For instance, the enormous numbers of beet leafhoppers produced on a stand of Russian-thistle and their scarcity on stands of downy chess. Also the large numbers of meadow mice that appear with a good cover of downy chess but the much smaller numbers in stands of Russian-thistle, mustards, or even perennial grasses. Then there are the plant-animal relationships involved in the differences in kinds and numbers of rodents in a cover of downy chess as compared to an adjacent one of native perennials, chiefly sagebrush and grasses. The practical significance of such relationships: to control an animal pest species by changing and improving the plant cover is scarcely appreciated and it has not been put into effect on any large scale. To get at these relationships there should be an experimental approach through complete protection of vegetation in all feasible ways (Piemeisel 1940) or through the method of no interference in any way as outlined by Shelford (1939) and embodying an area large enough to permit a natural development of even the largest native animals.

The need for a better understanding of plant communities has been stated by Watt (1947): "as things are, the current descriptions of plant communities provide information of some, but not critical, value to an understanding of them; how the individuals and the species are put together, what determines their relative proportions and their spatial and temporal relation to each other are for the most part unknown." These need to be known to understand the changes in the more stable, complex communities of perennials but also for the simpler communities of annuals, from their beginnings up to the more complex communities together with the corresponding changes in kinds and numbers of animals from insects, rodents and so on to the larger animals.

Summary

The communities that compose the greatest part of the vegetation of annuals on lands formerly occupied by sagebrush-grass are three: Russian-thistle, mustards, and downy chess. The three communities have an optimal arrangement as to the time when each appears and also the space each covers. This optimal arrangement is a potential that is realized on a cleared area if there is a negligible destruction of plants no matter by what cause and the entire discussion of processes is based on freedom from destruction. Russian-thistle dominates the greatest space the first two years; mustards, the third and fourth, and downy chess from the fifth year on. Within each of the communities there is a development best observed in one of downy chess and in an island somewhat removed from an established stand. This starts as a solitaire, a beginning age; then a cluster of a few individuals, the young age; then a dense stand, the mature age, and finally a very dense stand, the degenerate age. These age-groups are distinguishable in an island in color, height, and maturity (head emergency) as well as by density. If not disturbed the degenerate age is followed by a beginning or young age and a cycle sets in which may finally be cut short by a succeeding dominant, a native perennial. The age-groups may appear one a year though this is often cut short, depending on the position of the small area observed, with respect to an established stand. The changes from one community to another and the processes that take place within the community proceed in spite of differences in weather, years of above or below the av-

erage precipitation. Sparse stands mature and produce seed in years with precipitation below average and excessively crowded stands dry prematurely in years of above average precipitation. The spacing of the individuals within the groups, the degree of crowding, determines how the limited soil moisture supply of a unit area is to be shared by the individuals of that area. The soil moisture supply per individual is determined by the amount put into the soil (precipitation) and by the number of individuals (density) and of these two, precipitation varies by far the least. The communities thrive and reproduce themselves within the limits (high and low) of precipitation and the optimal arrangement (rate of change) can be realized within the limits of precipitation but is greatly disrupted by destruction of plants. Destruction may proceed slowly and imperceptibly over a series of years, each year's disturbance having its effect on succeeding generations. A better understanding will come with detailed studies of the communities free of any external disturbance as compared with those disturbed and when destruction each year is determined by appropriate measurements. This has a definite bearing on practical problems as well as on our fundamental knowledge of plant communities.

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OBSERVATIONS ON THE PENETRATION OF TIGHTLY CLOSING BIVALVES BY BUSYCON AND OTHER PREDATORS

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INTRODUCTION

There has been some doubt expressed as to the rôle of such tightly closing bivalves as *Venus, Ostrea, Modiolus, Mytilus,* and others in the diet of *Busycon.* Colton (1908) from observations of these gastropods in marine aquaria concluded that they may not be as serious predators of shellfish as previously reported. Warren (1916), watching predation of oysters and quahogs in the field, came to the conclusion that these bivalves constitute the chief articles of food of older *Busycon.* Clench (1939) observed penetration of a quahog in the field but considered such predation atypical. Magalhaes (1948) in her excellent monograph considered penetration of tightly closing bivalves a part of the normal feeding behavior of *Busycon.* Some baymen from estuaries along the New Jersey and New York coasts credit this snail with severe predation of oysters on bay bottoms. Thus *Busycon* captured by them in their tonging and dredging operations are thrown up on banks to perish or are utilized for food and bait. In view of these conflicting reports it has seemed desirable to report certain investigations on the method and extent of predation of the older stages of certain tightly closing bivalves by older *Busycon.* These studies have been conducted with *B. canaliculatum* Linné and *B. carica* Gmelin, first in closed running sea water systems in the Rutgers University Vivarium during the winter of 1948–49, and the following summer in the field in cages on a bar in Little Egg Harbor, N. J.[1] Similar predation studies with *Urosalpinx cinerea* Say and *Polinices duplicata* Say as well as incidental predation by *Callinectes sapidus* Rathbun in the field are also reported.

VIVARIUM STUDIES

Methods

Observations were begun in the fall of 1947 in a number of 10 gallon marine aquaria. These tanks were connected in series with large siphons permitting the circulation of imported bay water by means of a simple air lift pump placed at one end of the chain of aquaria. Further aeration was provided by the release of compressed air into each tank through thin cross sections of wooden dowel. Sand used in some of the aquaria was obtained at a local ocean beach. Clean bay water was collected in Shark River Basin, and in the Vivarium aquaria ranged in salinity in the course of the observations from 26.4 to 28.5 $^{0}/_{00}$. Water temperatures ranged from 17 to 25° C. Hydrogen ion concentration dropped after a few weeks from approximately 8.0 to 6.0 as metabolites accumulated in the water. Sodium bicarbonate was added to adjust the pH to about 7.5. No filter was required in the circulating sea water system since numerous bivalves provided excellent biological filtration. Six conchs, 4 knobbed (*B. carica*) and 2 channeled (*B. canaliculatum*) collected in Great Bay, N. J., and in Peconic Bay, Long Island, N. Y., were used in the experiments. The conchs ranged in length from 6.9 to 15.6 cm. and during the course of the observations, a period of some 8 months, the maximum growth added by any one conch at the shell lip was 10 mm. The

[1] The Vivarium studies were supported in part by a grant from the University Research Fund, Rutgers University. The field studies were conducted as a part of the Rutgers University Clam Farm Project supported by the Campbell Soup Company. Grateful acknowledgment is made for this aid.

maximum growth of shell added by any one oyster or quahog was 4 mm. Bivalve prey for the conchs was obtained in Shark River, with the exception of the oysters which were collected in Delaware Bay.

Method of penetration of bivalves

In an aquarium conchs creep at a relatively fast rate, 6 to 12 seconds per centimeter (Magalhaes 1948), attracted by the water pumped from the excurrent siphon of buried bivalves (also see Copeland 1918). Even deeply buried quahogs are readily dug out and attacked. As Warren (1916) has indicated, only the older *Busycon* are capable of attacking larger pelecypods.

Of all pelecypods, the *Venus*-like bivalves offer the greatest resistance to the predation of conchs, and yet these are readily penetrated and consumed. Although the method of penetration is essentially similar for all tightly closing bivalves, varying only with the size and thickness of the bivalve shell, it is in attacking *Venus mercenaria* Linné that these predators display most clearly their highly specialized mechanical method of opening bivalves. *Busycon* mounts the quahog and holds it, as Colton (1908) expressed it, "in the hollow of its foot," so oriented that the ventral edges of the quahog valves lie directly under the outer lip of the conch shell. Then the snail, by very slowly and strongly contracting the columellar muscle, brings the margin of its own shell to bear on the slight depression at the junction of the two quahog valves, and presses against the edge of the valve farthest from it (Fig. 1). Such force is generally sufficient to chip off a portion of the quahog shell. The gastropod then slowly relaxes, drawing its shell away from the quahog valves. This slow chipping is continued until an opening of sufficient size is effected to permit the conch to wedge its shell margin between the quahog valves. Warren (1916) recorded a rate of chipping of 6 times per minute on the oyster; a generally slower

FIG. 1. *B. carica* attacking *V. mercenaria*. The margins of the shells of the two animals are shown appressed at the termination of the chipping stroke. Approximately ⅓ ×.

rate has been observed in these studies. During the attack the snail occasionally interrupts its slow-motion hammering and exhibits a curious behavior: the edge of the anterior part of the foot, held just under the ventral rim of the valve to which the conch is adhered, is extended over the damaged area of the valves and numerous tiny lobe-like projections swell prominently and sweep undulatingly over the eroded shell as if in examination.

If the pressure brought to bear on the quahog valve by the conch is sufficient to crack loose a portion of the valve, as often happens, or if one or both of the valves crack from the pressure exerted by *Venus* in an attempt to remain closed, as occasionally occurs, the snail makes no attempt to force its shell between the valves. However, more commonly, repeated chipping is required to expose even a small opening. The snail attempts to wedge its shell between the valves as soon as an opening sufficiently large to permit penetration is chipped. Some victims, for

example, showed chipped holes only 0.5 mm. in width. The bluntness of the conch shell margin also determines the size of hole necessary for penetration, and this bluntness increases with the frequency and duration of attacks. The conch apparently adds new shell during resting periods when it generally remains buried in the bottom. Such rest periods have lasted as long as 16 days in aquaria; Colton found conchs to remain buried about 65 per cent of the time. Thus the conspicuous indented nature of the lines of shell growth in the conch is explained by the periodic erosion of the shell lip which occurs during attacks. The fact that most *Busycon* found by Clench possessed shells in perfect condition suggests that these snails were collected principally after the resting period.

In certain instances the chipping of quahog valves results, not in the formation of an opening, but in smoothing off of the edges of the valves, particularly of the valve edge farthest from the snail, and/or in the development of an opening too narrow to permit wedging. In such cases the predator eventually deserts the bivalve. In one such instance a conch worked alternately between two quahogs for seven days without penetrating either. Out of 37 quahogs which were placed with one large conch in one experiment, 15 quahogs were opened and 10 were attacked but could not be opened. In two cases a quahog showed two areas of attack, in which apparently the first attack had failed, and the second was successful. In 31 quahogs opened by conchs in one series of observations it was noted that 52 per cent of the sites of attack were located posteriorly over the siphons, 27 per cent over the midventral region, and 21 per cent over the anterior end.

It was reported to me by members of the crew of the oyster drill dredge boat *Quinnipiac,* during a trip on Peconic Bay, Long Island, that in the course of examining the material pumped off the bay bottoms and passed down the conveyer they had observed two cases in which large *Busycon,* still affixed to quahogs and with proboscides extended into the quahogs, also held the operculum wedged between the quahog valves. The use of the operculum in this way has not been observed during these experiments; it may well be a further means of aiding penetration.

Colton (1908), in his brief description of how a quahog is opened by a conch, wrote that there are three ways in which penetration may be effected: "First, it may flatten out its proboscis so that it will go through the crack; secondly, it may pour in a secretion between the valves which kills the clam; and thirdly, it may wedge its shell between the valves." The first and third ways mentioned by Colton agree with the observations herein reported; however, there is no evidence (nor did Colton present any) substantiating his statement that the conch may pour a secretion into the prey to kill it. Nor is there any evidence in this connection for Magalhaes' (1948) suggestion that the conch may initiate digestion externally. In some of the attacked but unopened quahogs in these observations, holes as large as 10×1.2 mm. were left with no signs of enzymatic secretions or of the possible lethal effects of such secretion. The quahogs were vigorous, healthy animals weeks later. Some observers have reported that the valves of pelecypods are pulled apart by suction of the foot. However, Magalhaes (1948) has demonstrated that a pull of 4 to 6 pounds is sufficient to dislodge a *Busycon* firmly attached to a surface, and Rees (1942) has estimated that a force of 23 to 26 pounds is required to force open a quahog. The penetration and consumption of tightly closing bivalves by *Busycon* is a purely mechanical phenomenon. Consumption of soft parts is accomplished by a physical rasping off and swallowing of bits of the mollusk flesh.

In attacking oysters, Colton suggests that the conch waits until the oyster opens and then inserts its shell between the valves. No such behavior was observed

in these studies. It is more likely, as Warren points out, that Colton's bivalves may have been weakened by life in the aquarium so that they opened while gripped in the foot of the conch. The ventral surface of the foot of the conch secretes a highly viscous mucus while attached to prey which plays a part in the great effectiveness of the conch foot in retaining its hold. Magalhaes' suggestion that this mucus is probably saliva appears unfounded. A *Busycon* once attached to a bivalve is not easily driven off. In these experiments pelecypods to which conchs were adhering were moved about and the conchs themselves handled with no effect on the conchs other than to cause them to draw their shells more closely upon the foot.

It was interesting to note that although bivalves are helpless against *Busycon*, small sea anemones on these shellfish are not such easy victims: one oyster on which a conch was creeping held a small *Diadumene luciae* (Verrill). As the foot came close to the anemone that portion of the foot nearest the coelenterate was suddenly withdrawn. The conch approached several times, each time retracting. Eventually it passed over the anemone, carefully elevating that portion of the foot over the anemone and keeping a safe distance from its nematocysts.

Rate and extent of predation in captivity

In a preliminary feeding experiment three small conchs were placed in an aquarium with an assorted collection of bivalves. Within 10 minutes each of the snails had a mussel enclosed in its foot; 4½ hours later these predators had penetrated and consumed 7 *Mytilus* (2.5–3.0 cm. long), 1 *Mya* (2 cm.), 1 *Ensis* (5 cm.), and 1 *Venus* (4 cm.). Throughout the conchs displayed a decided tendency to prey upon the thinner shelled mollusks first.

In the second feeding experiment six conchs were placed in an aquarium of slate bottom 23 × 12 inches, covered with about ½ inch of sand, in the presence of numerous bivalves. The temperature of the water remained in the vicinity of 20° C., and the salinity, 28 ‰. In the course of 23 days the following pelecypods were opened and consumed:

Mytilus edulis	1.5–4.0 cm. long	69
Venus mercenaria	2.0–5.0 cm. long	17
Mya arenaria	3.5–6.0 cm. long	3
Ensis directus	5.0 cm. long	1
Total number of bivalves consumed		90
Pelecypods consumed per conch per week		4.5

Conspicuous here is the fact that between the quahogs and the mussels which were present in about equal numbers, the conchs made greater inroads on the mussels.

In a third experiment five smaller conchs were placed in the same aquarium with about 100 oysters of various sizes. In a period of 99 days from December 29 to April 7 these conchs opened and consumed the following *Ostrea virginica:*

1.0–1.9 cm. long	28
2.0–2.9 cm. long	9
3.0–7.8 cm. long	22
Total	59
Oysters consumed per conch per week	0.84

In a fourth experiment the same five smaller conchs were placed in the same aquarium with about 150 oysters of various sizes. In a period from April 8 to May 8 for the five smaller conchs, and April 25 to May 8 when the largest conch was added to the tank, or a total of 163 conch days, these predators opened and consumed the following *O. virginica:*

1.0–1.9 cm.	33
2.0–2.9 cm.	18
3.0–6.6 cm.	12
Total	63
Oysters consumed per conch per week	2.7

The more than three-fold increase in consumption of oysters in the fourth experiment may be attributed to the increase in the temperature of the water. In the third experiment the temperature of the water remained between 18 and 20° C., whereas in the fourth experiment

the temperature stayed between 20 and 24° C.

In the fifth experiment it was hoped to check the extent of predation of quahogs that were permitted to bury in sand, since in the previous experiments the pelecypods were lying directly on the bottom, exposed to the conchs. The largest conch (*B. carica*) was placed alone in an aquarium with slate bottom, 2 × 1 feet in area, covered with approximately 2.5 inches of beach sand. Thirty-seven quahogs varying in length from 2 to 7.5 cm. were allowed to bury in the sand of the aquarium. In a period of 131 days, from December 15 to April 25, the conch opened and consumed 15 quahogs ranging in length from 3.3 to 5.6 cm. This is an average weekly consumption for the large conch of 0.86 *Venus*. In this same period 11 unsuccessful attacks were known to have been made on quahogs. If this figure is added to the 15 quahogs consumed, the potential consumption per conch per week becomes 1.4.

Field Studies

Animals and methods

Edge Cove Bar, Little Egg Harbor, N. J., was chosen as the site for these experiments. In addition to providing suitable bottom, water and water currents, sheltering a fair population of mollusks, being protected from excessive wave action, oil and small boat traffic, the Bar was readily accessible from the *Cynthia*, the Oyster Research Houseboat Laboratory of the New Jersey Agricultural Experiment Station. The *Cynthia* was moored in Thompson Creek approximately 500 yards from the Bar and supplied a base of operations for the summer's research on shellfish. A 26-foot power boat was used for work on the estuary and for towing the houseboat.

Edge Cove is a small arm of Little Egg Harbor which measures about 360 by 300 yards, and has an average water depth at mean low water of 3 feet. Two tidal creeks, Jeremy and Ezras Creeks, lead back into the marshes from the southwestern corner. The Bar extends about 200 feet into the Cove and measures some 40 feet in width. It is composed of a mixture of coarse and fine sand, shell and mud overlying the firm marsh mud with its entanglement of partly decayed grass roots and fine clay. The Bar rises about 1 foot above the normal contours of the Cove bottom. Two rows of old piling run out into the Cove along the Bar and afford some protection from wave action. Water currents pass over the Bar at approximately right angles to its long axis, and reach a current velocity at the peak of the flow during an average tide cycle of approximately 10 cm. per sec. A spot midway out along the Bar was selected for placement of the cages to house the predatory snails and the bivalve prey. The ground under the cages fell bare only during exceptionally low tides.

Meteorological conditions, tidal highs and lows, water temperatures, and salinities for the Edge Cove Bar area were recorded regularly throughout these studies, but are not reported in this paper.

Duplicate cages of galvanized screen supported by lath and corner stakes and embedded about 6 inches in the bottom were constructed for each of the predatory genera. For *Busycon* the cages consisted of 1-inch mesh chicken wire, 4 feet square and 1 foot high. The *Polinices* cages consisted of ½-inch mesh screen, 30 × 30 × 16 inches, and the *Urosalpinx* cages, of ¼-inch mesh screen, 3 × 2 × 1 feet.

Large quantities of the red alga *Polysiphonia variegata* (C. Agardh) Zanardini (kindly identified by E. T. Moul) adhered persistently to the cages during the summer and had to be removed periodically by wire brushing to maintain unimpeded circulation of the water through the cages. Even though severe wave action occasionally swept over the Bar, the cages remained in place and unharmed. The animals were placed in the cages on July 11 and were left there undisturbed for a period of 47 days to August 27 when the experiments were concluded.

Channeled conchs (*B. canaliculatum*) were found in large numbers over the bottom of Little Egg Harbor and in Thompson Creek in deeper water. An excellent indication of the abundance of these gastropods in an undisturbed area was obtained by J. M. Mott while preparing some bottom for us in connection with *Venus* plantings. In the period from August 15 to 24 he tonged an area 75 × 125 feet clean and collected a total of 91 large channeled conchs, an average of approximately 1 conch per 100 square feet. Local baymen cooperated in providing a few snails for these experiments, and it was learned during these contacts that although many of the baymen suspect the conchs of doing damage to shellfish, there are still those who return the conchs tonged by them to the water. The *B. canaliculatum* placed in the cages ranged in length from 6.9 to 21.5 cm. The *B. carica* used in the Vivarium studies were also utilized.

The moon snails, *Polinices duplicata,* were numerous on the bay side of the barrier beaches in the vicinity of Holgate. They were most easily collected during low water when their trails were visible in the sand. In one large tidal pool on this beach on two separate occasions a very large *P. duplicata* was unearthed from a depth of about 5 inches in the mud and sand where it had completely enveloped a large *Mya arenaria* and was feeding on it. Thus shallower burrowing forms like *V. mercenaria* may also be vulnerable to exposure and predation by this snail. *P. duplicata* used in the cages ranged in width from 2.4 to 5.7 cm.

Oyster drills, *Urosalpinx cinerea,* were present in some abundance along the west-

TABLE I. *Mollusks included in the 6 cages on Edge Cove Bar at the start of observations and their fate at the end of the 47 day period*

		Animals	Quantity at start	Fate of animals
Busycon:	(1) Mixed bivalves	*Modiolus*	300	All opened but 10.
		Ostrea	61	4 large and approx. half of current spat opened; drills native to Bar crawled into cages and destroyed remainder of spat.
		Venus	150	1 opened.
		Callinectes	1	Young specimen molted in cage, did not escape; opened 4 *Venus*.
		Busycon	8	All recovered.
	(2) *Venus* only	*Venus*	150	14 opened completely; 3 chipped, but still alive; 1 dead of unknown cause.
		Busycon	6	All recovered; 2 died early in observations so discounted.
Polinices:	(3) Mixed bivalves	*Modiolus*	250	120 drilled.
		Ostrea	43	None drilled.
		Venus	100	None drilled; 6 dead of unknown cause.
		Polinices	13	All recovered.
	(4) *Venus* only	*Venus*	100	11 drilled completely; no partial holes.
		Polinices	11	All recovered; 2 died early in experiment so discounted.
Urosalpinx:	(5) Mixed bivalves	*Modiolus*	200	All drilled.
		Ostrea	74	Half of large ones and all of spat drilled.
		Venus	50	None drilled; 8 dead of unknown cause.
		Urosalpinx	100	Of 94 recovered, 4 dead.
	(6) *Venus* only	*Venus*	50	One 35 mm. with 5 holes: 2 complete, 3 partial; 3 *Venus* dead of unknown cause.
		Urosalpinx	100	Of 59 recovered, 12 dead; remainder escaped through opening that developed in cage.

TABLE II. *New shell growth in millimeters added by the mollusks under the conditions existing in the six cages on Edge Cove Bar during the 47 day experimental period*

Cage	*Venus*	*Urosalpinx*	*Polinices*		*Busycon*	
	Maximum	Maximum	Maximum	Average	Maximum	Average
Urosalpinx mixed bivalves	7	10				
Urosalpinx Venus only	10	0.3				
Polinices mixed bivalves	5		20	10.3		
Polinices Venus only	5		6	1.0		
Busycon mixed bivalves	6				23	11.6
Busycon Venus only	5				23	14.0

ern shore of Little Egg Harbor, particularly on large pieces of marsh off the points of marshland. These portions of marsh sod are broken away by the undermining action of waves and fiddler crab tunneling, and being densely matted with *Modiolus demissus,* provide an attraction to the drills which feed on them. The high incidence of drilled bivalve shells on the bay bottom, including numerous early stages of quahogs, would indicate a fair population of drills there too. Adult drills, 20 to 30 mm. in length, were used in the experiments.

The quahogs placed in the cages varied in length from 1.5 to 7.0 cm., the smallest sizes being placed in the two *Urosalpinx* cages, the intermediates in the two *Polinices* cages, and the largest in the two *Busycon* cages. These quahogs were collected in Thompson Creek, on the Edge Cove Bar and in a large tidal pool near Holgate.

Three additional species of bivalves were placed in the control cages, and these were selected with consideration to thickness of shell and availability: *Mytilus edulis, Modiolus demissus,* and *Ostrea virginica. Mytilus* varying in length from 5 to 8 cm. were gathered on an old wreck near the eastern more saline portion of Little Egg Harbor; conditions on the western side of the Harbor in Edge Cove were apparently unsuitable because all perished in two or three weeks, and thus have been discounted in final tabulations. The combination of slightly reduced salinities and diminished water movement over them may account for their early mortality. The few that lived were entirely destroyed by the gastropods. *Ostrea* and *Modiolus* were collected in Thompson Creek and did well in the cages. The ribbed mussels varied in length from 2 to 8 cm., the larger forms predominating; the oysters varied in length from 2.5 to 15 cm.

Observations

The quantity of animals placed in the cages on July 11 and the fate of these animals at the end of the 47 day period is given in Table I. In Table II are given some data on the amount of new shell secreted by some of these mollusks in this same period.

Figure 2 illustrates typical cases of boring by *Polinices* and *Urosalpinx,* and Figure 3, chipping by *Busycon* and *Callinectes.* The more sharply beveled hole rasped by the moon snail is readily distinguished from the relatively straight sided hole drilled by the oyster drill. The results of chipping by the conch and by the blue crab are also distinguishable. The conch tends to wear the valve margins of a bivalve smooth, whereas the crab, since it penetrates by forcibly breaking off pieces of the valves with its chelipeds or by pressing its chelipeds between the valves, especially of smaller thick shelled pelecypods, generally leaves a jagged or roughly serrated breakage.

During the middle of the summer a small blue crab entered the *Busycon* mixed bivalve cage, moulted, and then could not escape. During the remainder of its stay it opened and consumed 4 quahogs. As

FIG. 2. Typical victims, from the predator-prey cages, of predation by *Busycon* on oysters, edible mussels, and quahogs, contrasted with (at right) results of attack by the blue crab, *Callinectes sapidus,* on quahogs. Approximately ⅓ ×.

shown in similar cage studies (unpublished) the blue crab is a significant enemy even of the thicker shelled bivalves: in one instance a caged 12 cm. crab in a 7-day period cracked open and consumed 6 *Venus* ranging in length from 3 to 4 cm. Nelson (1916) as early as 1915 made observations which led him to believe that the blue crab preys upon oysters. More recently Lunz (1947) has shown that the blue crab is perhaps the most serious of oyster pests.

FIG. 3. Typical examples of boring by *Polinices duplicata* in *Modiolus demissus, Polinices duplicata, Mytilus edulis,* and *Venus mercenaria,* contrasted with (at right) examples of drilling by the oyster drill, *Urosalpinx cinerea,* in *Ostrea virginica, Modiolus demissus, Mytilus edulis,* and *Venus mercenaria.* Approximately ⅓ ×.

The most striking observation disclosed by a study of Table I is that in the case of all three snail predators selection and penetration of prey correlated well with shell thickness. In all cases in the presence of mixed bivalves the thin shelled ribbed mussels were entirely or almost entirely consumed. The thick shelled quahogs were penetrated only in the absence of more easily attacked prey. As shown in Table II both *Polinices* and *Urosalpinx* grew as much as 10 times faster in the presence of mixed bivalves. In the presence of mixed bivalves *Busycon* consumed the thinner shelled bivalves almost exclusively, but it is to be noted that in this case, at least, they added a little more shell on the diet of *Venus* alone. On the average on the *Venus* diet alone *Polinices* consumed 0.15 quahog per week, and *Busycon,* 0.35 quahog per week.

Urosalpinx appeared to express no specificity of location in drilling *Modiolus;* holes were found on all parts of the shells. The only quahog that was drilled by the oyster drills, although several were kept from burrowing by the attachment of *Modiolus* byssus threads, contained 5 borings. Out of the 11 borings made in *Venus* by *Polinices* all holes were located on the umbones.

Discussion and Conclusions

The observations of Colton, Warren and Magalhaes that *Busycon* prey upon a variety of shellfish are amply confirmed by these studies. With minor exceptions the brief descriptions of Colton, Warren and Clench of the method of penetration employed by conchs fits the observations herein reported. The extent of predation on quahogs, oysters and mussels as studied under aquarium conditions, caged conditions in the field, as noted in random field observations and as related to the writer by local baymen, is, however, of much greater potential consequence than some of the earlier reports would indicate.

The following table gives the bivalve consumption per predator per week noted in these studies:

Location	Predator	Prey	Consumption
In aquaria	*Busycon*	Mixed bivalves	4.5 (fall)
In aquaria	*Busycon*	*Ostrea virginica*	0.84 (winter)
In aquaria	*Busycon*	*Ostrea virginica*	2.7 (spring)
In aquaria	*Busycon*	*Venus mercenaria*	0.86 (winter)
In field	*Busycon*	*Venus mercenaria*	0.35 (summer)
In field	*Polinices*	*Venus mercenaria*	0.15 (summer)

Greater consumption of quahogs by conchs in aquaria than in cages in the field may be explained by the fact that in aquaria no other food than quahogs was available to the snails, whereas in cages on Edge Cove Bar any one of the numerous organisms in the bay that could pass through the one inch mesh chicken wire became a possible food. Magalhaes points out that *Busycon* appear to be exclusively carnivorous, eating a varied diet that includes several species of pelecypods, annelids, and occasionally fishes and other gastropods. The aquarium studies also suggest that the temperature of the water is influential in determining the rate of feeding of conchs.

The field observations supply figures which can be used in calculating the potential degree of predation of quahogs by conchs. Considering 91 conchs (the total number collected in the 75 by 125 feet area on Edge Cove Bar), and the weekly rate of consumption of quahogs alone by a single conch as 0.35 (the rate of predation in the Edge Cove Bar cage), these 91 conchs, in the course of the five warmer months from May through September, could consume 700 quahogs.

That predation is generally not so severe is demonstrated by the decreased consumption of quahogs in the cages containing the mixed bivalves, where the thinner shelled bivalves were opened almost exclusively. Nevertheless, there are many acres of bottom in the local estu-

aries, Little Egg Harbor for example, where the bottom has been tonged and dredged for quahogs for decades, where conchs are present in some numbers and where the principal source of food is probably the quahog. The results of these studies indicate that predation of the quahog is probably higher on such bottoms than on a bottom harboring a mixed population including quahogs, oysters, *Pitar,* razor clams, and mussels. No observations are recorded on the extent of the damage inflicted by conchs on the edible mussel, but it may be postulated that the extensive *Mytilus edulis* beds occurring near the inlets of estuaries would provide a substantial food supply for *B. carica* which normally occur in bay water of high salinity.

These observations also demonstrate something of the protection from predation afforded the thicker shelled bivalves such as *V. mercenaria, Pitar morrhuana* and others, by the presence of the thinner valved mollusks such as *M. edulis* and *M. demissus.*

On a bottom populated principally by quahogs and bearing a comparable quantity and distribution of *Busycon, Polinices,* and *Urosalpinx,* these data point to the conch as the most serious enemy of the older stages of the quahog. It is not expected that the oyster drill would be a significant predator of larger quahogs, since drills do not generally burrow into the bottom during the summer months and quahogs dig into the bottom soon after the byssus thread is lost. However, random field collecting and systematic sieving of Edge Cove Bar bottom has disclosed a significant number of early *Venus* dissoconchs drilled by *Urosalpinx.* Young *Venus* through the end of the first summer of growth appear most vulnerable.

Polinices and *Urosalpinx* also exhibit a preference for the incompletely closing bivalves and/or the thinner shelled tightly closing pelecypods. In aquaria *Polinices* in the presence of both *V. mercenaria* and *M. edulis* did not attack a single quahog during the winter. In the absence of food it demonstrated considerable cannibalism. When only *Venus* were available as in the Edge Cove Bar cage, they were consumed, though the snails did not grow as well as in the presence of mixed bivalves. It would appear that *Polinices* is a more serious enemy of the young quahogs, and then only when there is a dearth of more easily penetrated food.

Of the predators here reported preliminary observations on the extent of penetration of quahogs by *Callinectes* suggest that this crab is an even more serious enemy than the gastropods, especially at those times of the summer when *V. mercenaria* migrates vertically through the bottom and remains near the surface.

Summary

1. Studies of the method of penetration of *Busycon canaliculatum* and *B. carica* and the extent of predation of *Venus mercenaria, Ostrea virginica,* and *Mytilus edulis* were carried out in large marine aquaria in the University Vivarium during the winter of 1948–49. The same bay water was circulated constantly through the tanks and salinity, temperature, and pH were checked periodically during the course of the investigation.

2. The method of penetration of tightly closing bivalves by *B. canaliculatum* and *B. carica* is described in detail and similar observations of previous investigators are confirmed and amplified. Penetration is a purely mechanical chipping and/or wedging apart of the shells of bivalves by combined synchronous action of the gastropod foot, columellar muscle, and shell.

3. Studies on the extent of predation of *V. mercenaria, O. virginica,* and *Modiolus demissus* by *B. canaliculatum, B. carica, Polinices duplicata, Urosalpinx cinerea,* and *Callinectes sapidus* in the field were conducted in cages on Edge Cove Bar, Little Egg Harbor during the summer of 1949. Air temperature, rainfall, water temperature, salinity and tidal height were recorded for the area in the

vicinity of the cages during the summer.

4. In aquaria predation of pelecypods by *Busycon,* expressed in terms of the number of bivalves consumed per week, was as follows: mixed bivalves (mostly *Mytilus* and *Venus*), 4.5; *Ostrea* (in the colder winter months), 0.84; (in the spring), 2.7; and *Venus,* 0.86. In the Edge Cove cages *Busycon* consumed 0.35 and *Polinices* 0.15 quahog per week.

5. In the case of all three snail predators the thinner shelled bivalves were selected and penetrated first. In the presence of *Venus* alone considerable predation of this mollusk took place. Thus some protection from such predation is afforded quahogs by the presence of thinner shelled bivalves. *Urosalpinx* and *Polinices* grew as much as 10 times faster on a diet of mixed bivalves; in the presence of mixed bivalves *Busycon* consumed *Modiolus* almost exclusively, but added slightly more shell on the diet of *Venus* alone.

6. Of the three gastropod predators studied, *Busycon* is the most serious enemy of the older stages of *Venus*. *Urosalpinx* is a serious enemy principally of the youngest dissoconch stages of *Venus*.

7. *Callinectes sapidus* is probably a more serious enemy of *Venus* than *Busycon*. In cages near Edge Cove the most voracious crab on the average opened and consumed almost a quahog a day for a period of 7 days.

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A COMPARISON OF VIRGIN SPRUCE–FIR FOREST IN THE NORTHERN AND SOUTHERN APPALACHIAN SYSTEM[1]

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Introduction

Extending down the crest of the mountains of the Appalachian system from Maine to Tennessee and North Carolina is a boreal type of coniferous forest dominated by spruce and fir. In the north, this montane spruce-fir forest merges more or less imperceptibly with the great boreal coniferous forest. Southward, the spruce-fir type is absent or poorly developed through the relatively low Allegheny Mountains of Pennsylvania, West Virginia, and Virginia. Farther south, however, in the high southern Appalachians, the spruce-fir forest is extensive and well developed, capping all the highest mountains and ridges. In the south, this forest reaches its best development in the Great Smoky Mountains where its boreal flora is surrounded on all sides by the complex, deciduous forests of the lower slopes and valleys.

The objective of the present study was twofold. Of first importance was the recording of the composition and structure of representative virgin stands of the Appalachian spruce-fir type as a part of a larger study of the boreal coniferous forest. Secondly, since it has been stated (Dice 1943) that the southern Appalachian spruce-fir forests are best considered as a part of the "Carolinian" biotic province, and that they "do not correspond very closely with any of the communities of the more northern provinces," comparisons were made between these southern spruce-fir types and similar forests in the northern Appalachians of New England. Such comparisons may be of value in establishing the historical development of the southern spruce-fir vegetation and in setting up any classification of vegetation of the southern Appalachian region.

Areas of Study

The best-developed and most extensive virgin forests of spruce-fir in the southern Appalachians are in the Great Smoky Mountain National Park. Here, because of trails and highways, many excellent stands are easily accessible. This region, from Mt. Sterling on the north to Clingman's Dome on the south, was, therefore, chosen as the southern area of study.

Selection of a similar area in New England was quite a different matter. The history of lumbering there (Oosting and Reed 1944) indicates that, since spruce has always been one of the most desirable timber trees, it was largely removed from accessible areas long ago. Virgin stands remain today only in fairly remote locations. Many of these stands are on poor sites occupying the shallow soils of extremely-steep slopes or subalpine locations not far below timberline. Modern equipment and recent high pulpwood and lumber prices have made it possible to cut many of these stands. Consequently, virgin spruce-fir in New England may soon be a thing of the past.

Since in 1946 there were still a number of virgin spruce-fir stands in the White Mountains of New Hampshire, and because U. S. Forest Service records

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were made available for locating them, the northern phase of the study was done there. It may be pertinent to add that lumbering was in progress here in more than one area which could otherwise have been used for study. In fact, one of the stands used in the study was being cut as the sampling was in progress. Other reported virgin stands, when located, were found to be too small for an adequate sample, of a successional nature, or of another forest type. As a result, in spite of advance information and assistance, it was possible to obtain data from only four good virgin stands in the time available. Fortunately, on the basis of results from the extensive virgin stands of the Smokies, these relatively-limited observations in the White Mountains appear to be adequate for comparison with the southern stands.

The airline distance between the two groups of stands is about 850 miles. The White Mountain stands are all fairly close to Latitude 44° N and Longitude 71° 30′ W, while the Smoky Mountain stands are in the region of 35° 30′ N and 83° 30′ W.

The stands which were studied are listed by number in table I, together with a distinguishing place name and topographic characteristics. By use of the place name, altitude, slope angle, and exposure, it should be easily possible for anyone to re-locate those in the Smoky Mountains. Those in the White Mountains are likewise designated by locally-familiar place names, but re-location would be more difficult. Stands 2N and 3N have in all probability been partially, if not completely, lumbered. Stand 1N was reached by starting on a marked trail (WMNF No. 300—"Tom Wiggin") from Wonalancet, N. H., and 4N was found at the head of a valley by following the Nancy Brook trail upstream.

TABLE I. *The stands used in the study with data on their positions*

Station	Elevation (in feet)	Slope	Exposure
Great Smoky Mountains			
1. Mt. Buckley	6,450	15°	N
2. Clingman's Dome	6,300	23°	N
3. Collins Gap	5,900	32°	SW
4. Sugarland Mt.	5,890	10°	N
5. Fork Ridge Trail, Mt. Collins	5,860	15°	S
6. Rocky Spring Gap	5,830	11°	N
7. Mingus Lead	5,450	30°	S
8. Le Conte Trail	5,700	25°	W
9. Mt. Sterling	5,600	15°	N
White Mountains			
1N. Mt. Whiteface	2,750	22°	NE
2N. Cascades Brook	2,500	25–30°	SW
3N. Livermore Pass	2,700	7°	W
4N. Nancy Brook	2,500	30–35°	N

METHODS

Field work on the project was done during the summer of 1946. Work was started first in the Smoky Mountains because of the great number of virgin stands there. It was intended that the study include enough stands to give the range of variation under different conditions of altitude, exposure, slope angle, and soils. When seven stands had been sampled quantitatively and presence data had been tabulated for two more, it was obvious that sufficient sampling had been done in the south to establish the characteristics of the type. It was desired that an equal number of stands be studied in the north; but, for the reasons previously stated, this was impossible; only four stands were sampled quantitatively in the White Mountains.

Each stand was sampled by methods similar to those used in previous studies of virgin coniferous forests (Oosting and Billings 1939, 1943). Two sets of quadrats were widely and evenly distributed through each stand at arbitrary intervals. One set consisted of ten quadrats each ten meters on a side. On these plots, all woody individuals of one inch DBH or more were counted and the DBH measured. The second set of quadrats was laid out in conjunction with the larger set and consisted of ten plots, each of

which was two meters on a side. On these plots, all woody plants under one inch DBH were counted; cover was estimated for herbs by species and for bryophytes collectively. In addition, a presence list was compiled of all species observed in the stand, both on and off the quadrats. A representative collection of bryophytes was made for later identification and addition to the presence lists. The moss and liverwort collections, now deposited in the Duke University Herbarium, were identified, respectively, by Dr. L. E. Anderson and Dr. H. L. Blomquist, of Duke University.

Before leaving a stand, increment borings were made at breast height on a representative series of size classes of the dominant tree species and the number of rings counted. The angle and direction of slope were measured and the elevation determined. Several small soil wells were dug in each stand to obtain samples of the organic and mineral horizons and to expose the profile for description.

After returning from the field, the quadrat data were analyzed for density, frequency, and basal area. At this time, specimens of herbaceous plants of doubtful identity were determined and samples of the underlying rock from each stand referred to type. Climatic information for stations closest to the stands was obtained from the yearly numbers of Climatological Data (U. S. Weather Bureau, 1938–1947).

Climate and Soils

Theoretically, similar climax vegetations should be indicative of similar climates. If this is true, a climate similar to that of the lower and middle slopes of the White Mountains should occur on the peaks and ridges of the Smokies at over twice the elevation of this climate in the north. Unfortunately, there are few weather stations located in the Appalachian spruce-fir vegetation. Of these few, only one in the north and one in the south have been in operation long enough for significant data to be available. Climatic data for the two stations are shown in table II, together with comparable data from Mt. Washington, N. H., located in the Appalachian alpine tundra and included to demonstrate the great climatic difference between similar topographic situations in the northern and southern Appalachians. Precipitation data only, from a new station on Clingman's Dome in the Smokies, are also included.

The only weather station in the north which is close, both geographically and in elevation, to the virgin spruce-fir stands studied is that at Pinkham Notch, N. H. This station is about 12 miles northeast of Station 4N (Nancy Brook) and about 500 feet lower in elevation. It could still be considered as in the spruce-fir climax area, but would probably have a slightly higher proportion of hardwoods in the virgin forest. The only useful records for the south are from Mt. Mitchell, N. C., in the Black Mountains some 60 or 70 miles northeast of the center of the southern study area in the Smoky Mountains. However, the climax vegetation and the elevation are comparable to the stands in the Smokies, and the climatic data are probably similar to those of the Smokies. There are two relatively new weather stations in the Great Smoky Mountain National Park, at which daily observations were begun in 1946. One is located at Newfound Gap near the lower edge of the spruce forest and the other at Clingman's Dome in the spruce-fir forest. Data for these stations are not yet available except some precipitation data from Clingman's Dome, which are included in table II.

The data from the two usable stations are surprisingly similar, considering their geographic separation. Mount Mitchell, in the south, is slightly warmer and wetter than Pinkham Notch in the north when the annual means are considered. However, Pinkham Notch is markedly colder in January than the top of Mt. Mitchell, with a mean of 16.9° F, as compared to 27.4° F for the southern station. Also, for the ten years 1938–1947 inclu-

TABLE II. *Comparative climatological data*

	J	F	M	A	M	J	J	A	S	O	N	D	Annual means	
(° F) T	27.4	26.5	31.8	39.9	49.2	56.4	59.3	58.4	54.8	45.6	35.7	29.3	42.9	Mt. Mitchell, N. C. 6,684 ft. at station
(in.) P	4.26	4.91	6.71	6.10	5.41	6.69	7.91	9.04	6.64	5.63	4.69	6.67	74.55	23-yr. record
P	7.29	9.35	10.06	4.98	7.08	8.65	10.11	7.47	5.28	2.27	17.87	8.43	98.43	Clingman's Dome, N. C. 6,400 ft. at station 1-yr. record (1948)
T	6.0	5.0	11.5	23.4	35.7	45.4	49.2	48.0	41.0	29.7	19.6	8.6	26.9	Mt. Washington, N. H. 6,262 ft. at station
P	5.93	5.48	7.20	6.95	5.72	6.26	6.10	6.15	7.48	6.27	6.41	7.07	77.02	14-yr. record
T	16.9	16.4	24.4	36.2	50.0	58.9	62.7	60.9	54.1	43.6	31.6	20.0	39.6	Pinkham Notch, N. H. 2,000 ft. at station
P	4.73	3.13	7.00	5.32	4.72	4.88	5.32	4.72	5.63	5.41	4.31	4.25	59.42	17-yr. record

	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947
Maximum temp. °F.										
Mt. Mitchell	78	77	81	77	78	79	79	80	78	76
Mt. Washington					67	67	71	66	67	71
Pinkham Notch	86	87	85	90	89	86	92	88	89	91
Minimum temp. °F										
Mt. Mitchell	−10	−10	−16	− 6	−10	−13	−10	− 9	0	−16
Mt. Washington					−45	−46	−28	−36	−37	−33
Pinkham Notch	−21	−18	−23	−10	−28	−32	−17	−18	−20	−11
Total snowfall (inches)										
Mt. Mitchell	46.0	46.6	69.8	47.7	105.5	44.1	67.5	99.6	21.1	58.7
Mt. Washington					147.8	183.0	134.2	163.4	137.4	190.6
Pinkham Notch	155.8	191.1	168.0	118.9	168.5	209.5	188.1	195.6	155.7	171.5

sive, the actual minimum at Pinkham Notch was lower in all but one year. The absolute minimum during this period for Mt. Mitchell was − 16° F, while Pinkham Notch had a low of − 32° F. Mt. Mitchell, however, is cooler in summer, with a July mean of 59.3° F, as compared with 62.7° F at the northern station.

Mt. Mitchell gets about 15 inches more of precipitation than Pinkham Notch. However, since precipitation increases with elevation, and since Pinkham Notch is below the spruce-fir stands in the north by 500 to 750 feet, it seems likely that precipitation in the stands studied would be nearer 65 inches per year. This would still show precipitation in the southern type to be somewhat higher than that in the north. Some of the stands in the Smokies probably receive more precipitation than Mt. Mitchell, however, since moist Gulf air-masses often have to rise over the Smoky Mountains from a southwest direction before entering the region of the Black Mountains. In 1948 precipitation on Clingman's Dome exceeded that on Mt. Mitchell by about 38 per cent and monthly totals were greater for all but two months of the year.

The precipitation at both northern and southern stations is fairly evenly distributed throughout the year. However, because of the lower winter temperatures, a much greater percentage of the precipitation in the north is in the form of snow. The mean annual snowfall for the ten-year period 1938–1947 at Pinkham Notch was 173.3 inches, while the mean for the same period at Mt. Mitchell was only 60.7 inches. It would seem that the heavier snowfall in the north coupled with lower winter temperatures would cause snowbanks to persist there longer, perhaps slowing the development of the her-

baceous vegetation. The snowpack in the north would also serve to insulate the perennial herbs and soil against the loss of heat to the colder northern winter air.

By comparing these climatic data with those from other climax vegetation areas in the east, it can be seen that the Appalachian spruce-fir forest represents what is probably the wettest and coldest climate in the region with the exception of the alpine tundra of the northern-most Appalachians. Data from the only station in this zone, Mt. Washington, appear in table II.

Although the soil observations were more or less superficial, the data (table III) give some idea of the nature and depth of the horizons making up the profiles, as well as the types of bedrock.

All of the rocks underlying the stands in the Smokies are metamorphosed. Gneiss, derived from granite, is the principal soil-producing rock here, with occasional outcroppings of quartzite and schist. In the north, all the stands were on light-colored granites.

In both the south and the north, the soils are shallow and rocky, with bedrock occurring between 50 and 80 centimeters below the contact between the organic and mineral horizons. In general, the soils are sandy, with the northern soils

TABLE III. *Soils*

Organic horizons					Mineral horizons			Type and depth of bedrock
Stat.	Total	L	F	H	Upper	Middle	Lower	
2	5 cm				0–12 cm black greasy	Yellow-brown	Brownish	At 55 cm probably gneiss
3	2–3 cm				0–10–12 cm black greasy	Cinnamon-brown	Yellowish-brown	At 50–70 cm schist, occasional quartzite blocks
4	3–5 cm				0–15–20 cm black greasy	Yellowish-brown grading to	Yellowish	At 50–60 cm probably gneiss
6	1–5 cm				0–10 cm black, greasy	Yellowish-brown between 10–70 cm	Sandier between 70–80	At 80–90 cm gneiss, some quartzite
7	5–7 cm				0–5 cm dark	Yellowish-brown down to 60 cm	Sandier with pieces of rock	At 75–80 cm gneiss
8	2–4 cm				0–5–10 cm dark	Yellowish-brown down to 45 cm	Sandier	At 50 cm gneiss
9	5–7 cm				0–5–10 cm gray-black	Yellowish-brown down to 30–35 cm		Gneiss
1N	25 cm	5	10	10	Absent?	Gray leached		White granite
2N	20 cm	5	5	10	0–15–20 cm black	Yellow-gray leached		At about 65 cm grayish-white granite
3N	10–20 cm	5	5	10	Almost absent	Yellow-gray		Grayish-white granite
4N	20 cm	5	5	10	0–10 cm dark	Gray strongly leached		Light-colored granite

being more so than those in the south. The organic horizons were always thick in the northern stands, ranging from about 20 to 25 centimeters deep. Litter (L), fermentation (F), and humus (H) layers were quite distinct. In the south, however, the organic layers were quite thin, ranging from about two to seven centimeters in thickness. It was difficult to detect the L, F, and H layers in these stands.

The mineral soil in the southern forests was always yellowish-brown in color. The upper part of this soil was almost black from the incorporation of organic matter into the upper mineral material thus forming a distinct A_1 horizon, which was underlain by the yellowish leached horizon. In the north, there was a sharp distinction between the organic horizons and the mineral horizons. In two of the stands, the humus layer was immediately over a grayish leached A horizon, while in the other two stands there was some evidence of a darker A_1 horizon between the organic layers and the strongly leached, gray A_2 horizon. In both the north and the south, the soils are evidently true podzols, but the southern examples have thin organic layers and yellowish leached horizons, probably reflecting their slightly milder climate. However, podzolization and organic horizons may be much more highly developed than this in the south. Coile (1938) found such podzols under red spruce in West Virginia, where the parent material is sandstone or sandstone conglomerate. He described A_0 horizons whose depth exceeds 12 inches on highly siliceous, poorly drained soils and pointed out that such development is not found on the metamorphic and igneous rock of North Carolina and Tennessee.

Vegetation

General survey

Presence.—In describing and comparing the vegetation in several stands of a climax virgin forest, the logical first step is to list all the species present in these individual stands. This is a distinct aid in determining characteristic species and formulating concepts in regard to the uniformity and variation of the community. At the same time, it provides a first basis for comparing the floristics of the community in two different regions where certain similarities are known to exist but the degree of similarity is only surmised. This material has been brought together in table IV, which indicates the presence of arborescent, shrubby, and herbaceous species at nine spruce-fir stations in the Great Smoky Mountains in the south and at four similar stations in the White Mountains in the north.

No more than casual inspection is necessary to see that three groups of species are represented. Whether trees, shrubs, or herbs, there is one group which is present in the north and the south, with extremely high presence values in both regions. A second group is found only in the south, and a third group occurs only in the north.

Among the trees, *Picea rubens* and *Betula lutea* are present throughout as dominants. The understory species, *Sorbus americana* and *Acer spicatum,* are also present in almost every stand. Fir is consistently present but as *Abies fraseri* in the south and *A. balsamea* in the north. Additional tree species of high presence for the north are *Betula papyrifera* and the subordinate tree, *Acer pensylvanicum,* while *Prunus pensylvanica* may be expected as a frequent associate in the south.

Only two shrubs occurred as binding species. *Viburnum alnifolium* is present throughout and *V. cassinoides* occurs occasionally. The sparse shrub layer of the north included only one other species (*Nemopanthus mucronata*) that was found in more than one stand but in the south there were three additional species present in almost every stand (*Vaccinium erythrocarpum, Rubus canadensis, Sambucus pubens*).

The presence values of herbs serve to accentuate both the similarity and distinctness of the two geographic forms of

TABLE IV. *Tabulation of presence of species of trees, shrubs, herbs, and bryophytes in the nine southern and four northern spruce-fir stands*

	Great Smoky Mts.									White Mts.			
	1	2	3	4	5	6	7	8	9	1	2	3	4
Trees													
Picea rubens Sarg.	x	x	x	x	x	x	x	x	x	x	x	x	x
Betula lutea Michx.	x	x	x	x	x	x	x	x	x		x	x	x
Sorbus americana Marsh.	x	x	x	x	x	x	x	x	x	x	x	x	x
Acer spicatum Lam.		x	x	x	x	x	x	x	x	x	x	x	x
Abies fraseri (Pursh) Poir.	x	x	x	x	x	x	x	x	x				
Prunus pensylvanica L.			x	x		x		x					
Ilex monticola A. Gray							x						
Fagus grandifolia Ehrh.							x						
Abies balsamea (L.) Mill.										x	x	x	x
Betula papyrifera Marsh.										x	x	x	x
Acer pensylvanicum L.										x	x		x
Tsuga canadensis (L.) Carr.													x
Prunus serotina Ehrh.											x		
Shrubs													
Viburnum alnifolium Marsh.	x	x	x	x	x	x	x	x	x	x	x	x	x
Viburnum cassinoides L.							x				x		
Vaccinium erythrocarpum Michx.	x	x	x	x	x	x	x	x	x				
Rubus canadensis L.	x	x	x	x	x	x	x	x	x				
Sambucus pubens Michx.	x		x	x	x	x	x	x	x				
Ribes rotundifolium Michx.	x							x					
Rhododendron catawbiense Michx.									x				
Vaccinium pallidum Ait.							x						
Nemopanthus mucronata (L.) Trel.												x	x
Vaccinium pensylvanicum Lam.													x
Rubus sp.												x	
Ribes sp.													x
Herbs													
Aster acuminatus Michx.	x	x	x	x	x	x	x	x	x	x	x	x	x
Dryopteris dilatata (Hoffm.) Gray	x	x	x	x	x	x	x	x	x	x	x	x	x
Oxalis montana Raf.	x	x	x	x	x	x	x	x	x	x	x	x	x
Clintonia borealis (Ait) Raf.	x	x	x	x	x	x	x	x	x	x	x	x	x
Monotropa uniflora L.		x	x	x			x	x	x		x	x	
Trillium undulatum Willd.		x		x			x	x	x	x			x
Carex flexuosa Muhl.	x	x	x		x				x	x	x		
Lycopodium lucidulum Michx.		x	x				x			x	x	x	
Cinna latifolia (Trev.) Griseb.			x		x		x			x			
Viola rotundifolia Michx.								x	x		x	x	
Dryopteris intermedia (Muhl.) A. Gray							x					x	
Streptopus roseus Michx.	x											x	x
Senecio rugelia A. Gray	x	x	x	x	x	x	x	x					
Houstonia serpyllifolia Michx.		x	x		x		x						
Solidago glomerata Michx.	x	x	x		x								
Aster divaricatus L.			x	x	x								
Impatiens pallida Nutt.	x	x					x						
Chelone lyoni Pursh	x	x						x					
Arisaema quinatum (Nutt.) Schott.		x				x							
Circaea alpina L.	x		x										
Stachys clingmanii Small		x											

TABLE IV—*Continued*

	Great Smoky Mts.									White Mts.			
	1	2	3	4	5	6	7	8	9	1	2	3	4
Herbs—*Continued*													
Cornus canadensis L.										x	x	x	x
Maianthemum canadense Desf.										x	x	x	x
Aralia nudicaulis L.										x	x	x	x
Solidago macrophylla Pursh										x	x	x	x
Coptis trifolia (L.) Salisb.												x	x
Trientalis americana (Pers.) Pursh											x	x	
Dryopteris hexagonoptera (Michx.) C. Chr.											x	x	
Chiogenes hispidula (L.) T. & G.													x
Mosses													
Brotherella recurvans (Mx.) Fleisch.		x	x	x	x	x	x	x	x	x	x	x	x
Dicranum fuscesens Turn.			x	x		x		x		x	x	x	x
Dicranum scoparium Hedw.		x		x		x			x		x	x	x
Tetraphis pellucida Hedw.			x		x		x	x			x	x	x
Brotherella delicatula (James) Fleisch.				x			x	x	x		x	x	
Dicranum montanum Hedw.				x				x		x			x
Eurhynchium serrulatum (Hedw.) Kindb.					x				x			x	
Dicranodontium denudatum (Brid.) E. G. Britton		x	x	x	x	x	x	x	x				
Hylocomium splendens (Hedw.) Bry. Eur.		x	x	x	x	x	x	x	x				
Thuidium delicatulum (Hedw.) Mitt.				x	x	x	x	x	x				
Atrichum undulatum (Hedw.) Beauv.		x		x	x		x	x					
Polytrichum commune Hedw.		x	x		x	x			x				
Brotherella tenuirostris (Schimp.) Broth.			x	x	x	x			x				
Hylocomium brevirostre (Beauv.) Bry. Eur.								x					
Rhytidiadelphus triquetris (Hedw.) Warnst.									x				
Hypnum crista-castrensis Hedw.									x				
Paraleuchobryum longifolium (Hedw.) Loeske													
Dicranum fulvum Hook									x				
Campylium chrysophyllum (Brid.) Bryhn			x										
Pohlia elongata Hedw.		x											
Dicranella rufescens (Smith) Schimp.		x											
Plagiothecium muellerianum Schimp.			x										
Calliergonella schreberi (Brid.) Grout										x		x	
Polytrichum ohioense Ren. & Card.											x		x
Cratoneuron filicinum (Hedw.) Broth.											x		
Homomalium adnatum (Hedw.) Broth.											x		
Leucobryum glaucum (Hedw.) Schimp.													x
Dicranum rugosum (Hoffm.) Brid.													x
Plagiothecium denticulatum (Hedw.) Bry. Eur.													x
Sphagnum squarrosum Crome													x
Sphagnum girgensohnii Russ													x
Liverworts													
Bazzania trilobata (L.) S. F. Gray		x	x	x	x	x	x	x	x	x	x	x	x
Lepidozia reptans (L.) Dum.			x				x	x		x	x	x	
Tritomaria exsecta (Schmid.) Schiffm.		x		x	x	x		x					
Frullania asagrayana Mont.		x	x	x			x						
Cephalozia curvifolia Dum.		x	x			x		x					
Cephalozia media Lindb.		x	x		x	x							
Herberta tenuis Evans			x		x	x							
Cephalozia connivens (Disks.) Lindb.		x											
Lophozia inflata (Huds.) M. A. Howe			x										
Blepharostoma trichophyllum (L.) Dum.			x										
Jamesoniella autumnalis (DC.) Steph.								x					
Ptilidium pulcherrimum (Web.) Hampe										x			x
Cephalozia bicuspidata (L.) Dum.										x			
Lophozia porphyroleuca (Nees.) Schiffn.										x			
Plectocolea fossombronoides (Aust.) Mitt.											x		
Calypogeia neesiana (C. & M.) K. Mull.												x	

the montane spruce-fir forest. Twelve species are found in both the north and south and, of these, four were found at every station. These universal species of high presence were *Aster acuminatus, Dryopteris dilatata, Oxalis montana,* and *Clintonia borealis.* Four other herbs were found at not less than half of all the stations. The nine species found only in the southern stands include several that are endemic in the Smoky Mountains. Of these endemics, *Senecio rugelia* was constantly present. Eight species occurred only in the north of which four were present in every stand examined in that region. These four were *Cornus canadensis, Maianthemum canadensis, Aralia nudicaulis,* and *Solidago macrophylla.*

The collectors' relative lack of familiarity with the bryophytes could affect to some extent the data obtained on their presence. However, the fact that the tabulations of their occurrence conform with those obtained for vascular plants seems to justify the method and substantiate general conclusions. Here also, for both mosses and liverworts, are groups of species with high presence values occurring in both the north and the south and other groups restricted to each of the two regions. The rich bryophytic flora of the Smoky Mountains is reflected in the relatively long list of species found in the stands there (33 versus 23 in the north). The generally favorable conditions for bryophytes in the south are indicated also by the greater number of species which were found in over half of the stands. Sixteen bryophytes were in this group in the south as against nine in the north.

Detailed lists of the bryophytes found in the major communities of the Smokies are available (Cain 1935; Cain and Sharp 1938). These were obtained by intensive methods to show relationships to substrate and the groupings of species. By comparison, the present presence list appears quite representative.

Presence diagrams (fig. 1) serve to

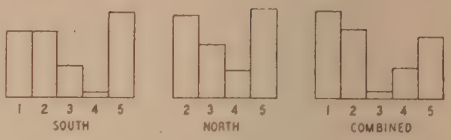

FIG. 1. Presence diagrams for the vascular plants of the two areas of study and a combined diagram. No species could fall in class 1 in the north because only four stands were involved.

emphasize the high proportion of species which are constantly present. Whereas most communities have a very high proportion of species in class 1 (rare) and tend to have declining sizes of succeeding classes, 33 per cent in the southern stands are constantly present. Usually a presence diagram shows no second maximum because of the relatively small number of constantly present species. Even when presence data for north and south are combined the form of the diagram remains the same. There are 42 species represented in the southern stands, 37 in the north and only 59 in the combined values. Obviously, the vascular flora is not rich in species and there is great similarity in the two floras as evidenced by the fact that 60 per cent of all species are found in both the north and the south.

Constance.—Single unit sampling areas for constance were not used but a good measurement of constance is obtained by combining the multiple sample plot data obtained in each stand and treating it as though it were from a single large quadrat.

On this basis, only 47 species are significant (i.e., occurred in sample areas and therefore usable in the computation) in the entire range and, among these, 34 occur in the south and 27 in the north. Only 30 per cent (14 species) are found in both parts of the range. Since 40 species actually occur (on the basis of presence), it is apparent that a high proportion of those extending throughout the range are incidentals or of little significance in the community.

Constance diagrams (fig. 2) have a greater resemblance to normal than those

for presence. The proportion of species with high constancy is considerably reduced but the fact remains that, in the south at least, an unusually large part of the flora is constant. Although the diagram for the north is irregular it indicates a greater resemblance to normal distribution of constancy groups.

Cover-stratification.—The general similarity of the northern and southern forest as well as certain differences become especially apparent in cover-stratification diagrams (fig. 3).

The dominant tree stratum, made up of three species in the south and four in the north, is equivalent in the two areas but the average height of the forest is somewhat greater in the south. There are only four subordinate woody species in the south, two of which also occur in the

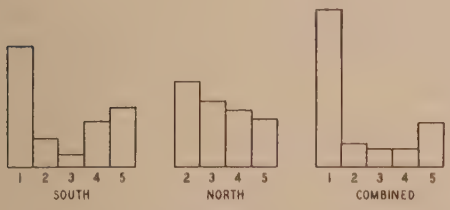

FIG. 2. Constancy diagrams for stands in the two areas and for the areas combined.

north where there are five species. Their relative insignificance is indicated by their low cover class (less than five per cent).

Shrubs, which in both areas may be up to ten feet tall, do not exceed cover class two. However, there is somewhat greater diversity of species in the south.

Although the number of herbs is only slightly greater in the south, their average coverage is about twice as great as that of those in the north. Bryophytes too make a greater cover in the south. The greater cover of these lesser species and also the greater height of trees suggests that growing conditions are generally more favorable in the south.

Cain's (1935) cover-stratification diagrams are similar to these but differ particularly in the much greater height of

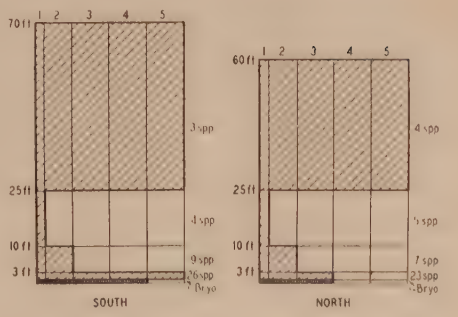

FIG. 3. Cover-stratification diagrams for virgin spruce-fir forest in the southern and northern Appalachians.

spruce and the limit of 50 feet for fir. Part of this discrepancy may result from a difference of interpretation of mean mature height. But, the difference also lies in his representation of a spruce-dominated stand at relatively low altitude and an essentially pure stand of fir such as is found on poor sites at the highest altitudes. Our diagrams supposedly represent an average of numerous mixed stands such as are found at middle altitudes in the zone. Brown's (1941) diagram for spruce-fir on Roan Mountain is for the same mixed association and is more in agreement.

Stand analysis

Frequency.—Diagrams for individual stands are extremely variable and only a few have the "normal" form. Class E is rather consistently high because of the high proportion of constant species (largely dominants) present with high frequency. This, in combination with a large value for class A, is commonly taken to indicate extreme homogeneity. But, class A is not consistently high for all stands and B, C, and D show irregularities. From other data it is apparent that the dominant species in each stratum are uniformly distributed and always present but lesser species occur within a stand with no great consistency.

In composite diagrams for the north and south (fig. 4) the irregularities of

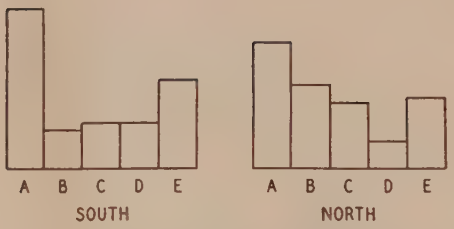

FIG. 4. Composite frequency diagrams indicating average frequencies by classes for all southern and northern stands.

individual stands are eliminated and both show a closer approximation to the normal form. The northern composite diagram, however, like the individual diagrams, still indicates a lesser homogeneity because of the relatively greater size of classes B, C, and D.

Within the two regions or otherwise there is no apparent correlation between the inconsistencies of the diagrams and altitude or exposure. Neither does the number of species found in the plots in a stand (variation from 8 to 32) have a consistent effect on the form of diagram.

Density and basal area.—Spruce and fir are the two major trees involved in this study. Therefore their quantitative values may well be considered on a comparative basis between stands and regions. Phytographs comparing the species by stands (fig. 5) show a high degree of similarity.

In the south, stand 7 is irregular as is stand 4N in the north. If these be ignored for the moment it is immediately obvious that Fraser fir regularly is three to five times as abundant as spruce in the southern stands and that balsam fir tends to be present in greater numbers than spruce in the north but not by so great an amount.

Although the number of fir trees over an inch in diameter is generally greater than that of spruce trees, the total basal area of fir tends to be substantially less than that of spruce. Thus the spruce

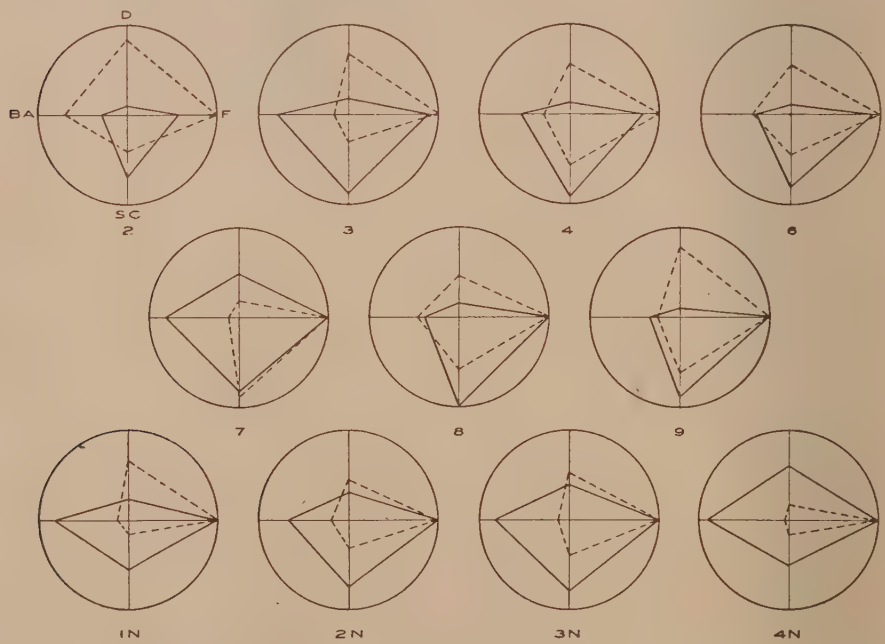

FIG. 5. Phytographs showing comparative density, frequency, basal area, and size classes (expressed as per cent of maximum size of largest tree in any stand) of spruce (——) and fir (- - -) in each of the stands studied intensively. Numbers 2–9, southern; 1N–4N, northern.

trees, on the average, are much larger than the fir.

The relatively low density of spruce occasionally produces a frequency of less than 100 per cent but fir trees an inch or more in diameter were found in every plot in every stand.

Size classes in these phytographs have a somewhat different basis than commonly used. They are expressed by two-inch diameter classes in percentage of the largest tree encountered on any plot (34 inches). Thus spruce in stand 8 ranged through size classes up to and including 34 inches DBH, while spruce in stand 1N ranged through only 61 per cent of the maximum possible size classes —namely, from one to 20 inches. This makes it possible to compare the range of tree-sizes directly from stand to stand. Invariably individuals in size-classes up to 10 inches are well represented. Beyond this size the fir representation is extremely irregular but spruce tends to have a few individuals in almost every two-inch class up to the maximum for the stand.

Some of the irregularities in figure 5 should be explained. Stand 2 was at an altitude of 6,300 feet, the highest of any stands worked intensively. Factors associated with altitude are undoubtedly involved in the changing of the relative importance of spruce and fir. With increasing altitude, spruce decreases in numbers and size and, not infrequently, fir occurs in almost pure stands on the highest ridges.

Phytograph 7 is irregular because of an unusually large number of spruce in the 1–4 inch diameter classes. This spruce competition perhaps kept the number of small firs below normal. In spite of a rather normal distribution of both spruce and fir individuals in other diameter classes the relative density is thus somewhat out of line. A single Fraser fir with a diameter of 30 inches accounts for the extension of range of size classes to 88 per cent of the maximum. The next largest fir tallied in the stand was only 18 inches DBH. In fact, the next largest fir found in any stand in any plot was 22 inches. Phytograph 4N is also distorted by an abnormally high count of spruce in the 1–4 inch diameter classes combined with a relatively low number of fir in these same classes.

The absolute values for density, basal area, and occurrence by diameter classes are presented in table V. Here it becomes apparent that it is characteristic for spruce to be present in small numbers in each of a wide range of diameter classes and for fir to occur in higher numbers but in a much more limited range of sizes.

Average density of spruce is three times as great in the north as the south but total basal area averages only 62 per cent greater (table V). The difference lies in the concentration of spruce in the three lowest diameter classes. The maximum diameter of spruce measured in the north was 26 inches and, in two stands, it was no greater than 20 inches. This is in contrast with a range of maxima from 28 to 34 inches in six stands in the south and a low maximum of 24 inches in only one stand.

Fir, too, has a higher average density (46 per cent greater) in the north but its average basal area is only 39 per cent of that in the south. The difference is clarified when it is noted that maximum diameters of balsam fir were in the 4, 6, 10, and 12-inch classes for the four northern stands while maxima for Fraser fir ranged from 10 to 30 inches.

Seedlings (less than 1 in. DBH) of both spruce and fir were produced in greater numbers in the north than the south. Spruce seedlings in the Smoky Mountains were tallied with an average density of 26.1 (per 100 sq m) as compared to 202.5 in the White Mountains. Density of Fraser fir seedlings averaged 108.3 (per 100 sq m) while balsam fir was 137.5. The high production of seedlings in the north accounts for the high stocking in the low diameter classes and, probably, because of the resulting generally high density, it contributes to the

TABLE V. *Numbers, by two-inch diameter classes, total numbers, and basal area of spruce and fir found in ten 10 × 10 meter plots in each of the stands, and the relation of these values to the totals for all species*

Stand	Repr. —1	1-	2-	4-	6-	8-	10-	12-	14-	16-	18-	20-	22-	24-	26-	28-	30-	32-	34-	Total 1" plus	% total all spp.	BA sq. ft.	% BA all spp.
Smoky Mts.																							
2	125	1	2	3	5	4	1	1	2					2				←spruce		21	12.7	14.5	28.8
	3850	12	22	37	31	20	10		2									←fir		143	86.1	35.1	69.9
3	725	8	3	1	1		1	1	4	5	1	3	5	2	3		1			39	21.0	63.1	77.7
	725	25	52	29	15	6	5													131	70.4	15.4	19.0
4	375	12	9	2		2	2			2			1	2	3	2	1			38	16.7	42.1	53.6
	525	47	63	7	11	3		5	2	1	2	1								141	61.8	22.4	28.5
6	400	7		1		1	1	1	2	1	2	1	1	1		1				21	15.8	23.5	37.8
	1525	12	18	10		8	9	1	5	1		1								81	60.9	23.7	38.2
7	100	74	60	7	4	1	3	1	5	1	4			5		1				170	54.3	50.1	83.0
	100	16	33	16	2		2				1						1			72	23.0	7.2	11.9
8	0	7	13	8	3	2		1		1	1	1		2					1	41	19.6	23.1	35.9
	150	36	38	8	3	6	7	4	4	2		1	1							112	53.6	28.4	44.2
9	100	9	4	1		2	1	2		1			1	2			1			25	11.3	20.4	35.8
	700	68	61	23	14			4	1				1							172	77.8	16.5	28.9
Aver.	261	17.1	13.0	3.3	1.9	1.7	1.3	1.0	1.9	1.6	1.1	0.7	1.1	2.3	0.9	0.6	0.4		0.1	5.1	21.6	33.8	50.4
	1082	30.1	40.7	18.6	10.9	6.1	9.8	2.0	2.0	0.6	0.4	0.4	0.3				0.1			12.1	61.9	21.2	34.4
White Mts.																							
1N	1650	42	7	6	12	7	14	12	8	5	3	2						←spruce		124	27.1	57.6	85.6
	2650	185	149	1														←fir		334	72.9	6.9	10.3
2N	1450	31	24	12	6	4		2	1	3	3	2	2	3	3					98	35.6	53.5	68.5
	800	37	56	30	14	10	1													132	48.0	13.2	16.9
3N	2300	63	29	12	8	4	8	5	6	3	5	3	1	3	1					150	43.2	62.3	79.2
	1350	66	43	32	4	6		2												178	51.3	11.4	14.5
4N	2700	120	48	20	10	8	11	13	7	2	3									245	65.3	46.4	88.4
	700	29	29	3	1															62	16.5	1.8	3.4
Aver.	2025	64	27	12.5	9	5.8	8.3	8.0	5.5	3.3	3.5	1.8	0.8	1.5	1.0					15.4	42.8	54.9	80.4
	1375	104	77	16.5	4.8	4.0	0.3	0.5												17.7	47.2	8.3	11.3

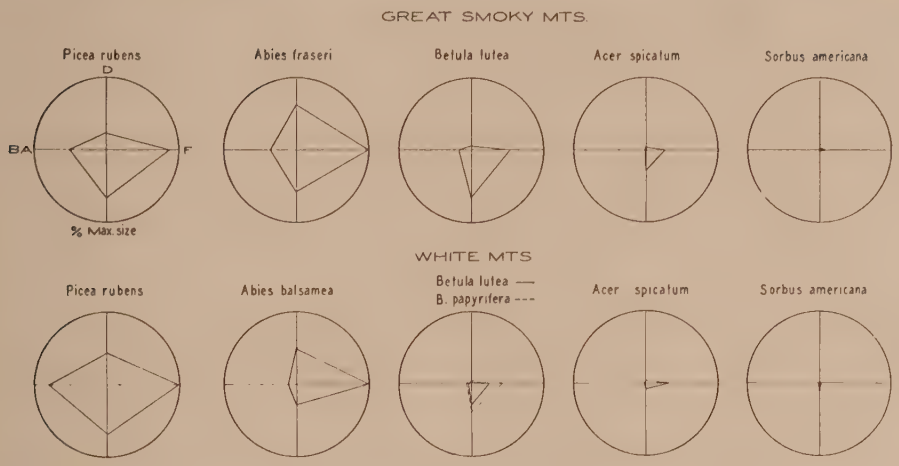

FIG. 6. Composite phytographs for comparison of density, frequency, basal area, and range of diameter classes of trees in the southern and northern stands.

greater restriction on size as compared to the south. It would appear that balsam fir does not have as great an ability to compete with spruce as does Fraser fir but the two situations are not entirely comparable. Although density of balsam seedlings averages slightly greater than that of Fraser fir seedlings the balsam must compete with six times as many spruce of seedling size and spruce has a high survival value.

Composite phytographs (fig. 6) of the principal species of trees further clarify the above discussion of spruce-fir relationships and, additionally, show the significance of associated species.

It is apparent that birch must be recognized as making up a small but significant part of the community. In the south, density of yellow birch constitutes 5.1 per cent of the total for all trees and the species makes up 15.8 per cent of the total basal area. Birch is present in all diameter classes and many trees are large, often 20 inches in diameter or more. Although birch frequency averages only 54 per cent as contrasted with nearly 100 per cent for conifers, the birch rarely drops much below this value.

In the northern forest both paper birch and yellow birch are present. Apparently paper birch takes over a part of the position held by yellow birch in the south for their combined values for the White Mountains are similar to those for yellow birch in the south. Paper birch has

TABLE VI. *Average density and frequency of shrubs in southern and northern stands*

	Average density		Average frequency	
	South	North	South	North
Viburnum alnifolium	1.4 (0–4.8)	1.8 (0–2.8)	32.0 (0–70)	32.5 (0–50)
Sorbus americana	0.2 (0–0.7)	1.5 (0–5.1)	11.8 (0–40)	32.5 (0–70)
Vaccinium erythrocarpum	1.0 (.1–5.4)		41.4(10–80)	
Rubus spp.	1.1 (0–3.1)	0.13 (0–.5)	18.6 (0–50)	0.5 (0–20)
Sambucus pubens	0.1 (0–0.1)		.01(0–10)	
Vaccinium pallidum	0.01(0–0.1)		.01(0–10)	
Nemopanthus mucronata		0.05 (0–.2)		.05(0–10)
Total	4.59	3.44	Aver. 17.48(0–80)	16.39(0–70)

a somewhat higher density, a greater basal area, is represented by larger trees, and is more uniformly distributed. Nevertheless, neither species in the north attains the size of birch in the south and, although their combined density in the north (12.5 per 100 sq m) exceeds that of yellow birch in the south (11.6) basal area of yellow birch in the south averages (9.19 sq ft per 100 sq m) almost double that of the two species in the north (4.94).

Woody species other than *Acer spicatum* and *Sorbus americana* occur too irregularly or have such relatively low values that phytographs are meaningless. Note that these two species have much the same position in both northern and southern communities. In the south, Acer is apt to be a slightly larger tree and Sorbus occurs with greater regularity.

Age, growth, and longevity of trees.— A systematic attempt was made to get increment borings from representative trees of spruce and fir in every stand. Because of the size of some of the larger trees it was not always possible to get borings complete to their centers. Others were sometimes rotten at the center and consequently ages for such trees could only be approximated.

At times it appeared that age and amount of growth had little relationship. Although generally the largest trees were the oldest this was not by any means always true. Overstocking results in slow growth rates, overtopped individuals of both spruce and fir may live suppressed for long periods (50 years or more) and, when released by the death of an old tree in the crown, may then grow very rapidly for a time. Trees of the same size in a stand may have widely different ages and large and small trees may be of the same age.

In spite of these apparent irregularities, graphs of the number of rings plotted against diameters (fig. 7) permit some rather definite generalizations. It appears that growing conditions for spruce and fir are more favorable in the south

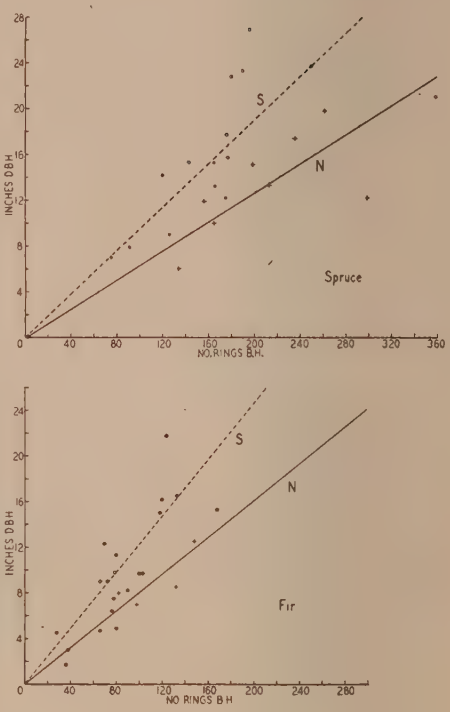

FIG. 7. The rate of growth of spruce and fir as indicated by plotting diameters at breast height against the number of growth rings.

than the north because spruce shows a better growth rate there and Fraser fir grows more rapidly than balsam fir. Likewise, it is apparent that both firs grow more rapidly than red spruce, regardless of geography.

As would be expected in virgin stands, all were decidedly uneven-aged and this includes the trees of the overstory which vary as much as 200 years. The oldest tree for which an accurate count was obtained was a spruce on Clingman's Dome only 21 inches DBH but which had produced 359 rings. Other spruce over 20 inches were more commonly 200 to 250 years old in the south. The oldest accurate count in the north was made on a 12.2 inch spruce which was 299 years of age. Other borings of spruce in the north suggested that 200 to 250 years commonly may be required for spruce to

grow to 15–20 inches DBH. Although the growth rate of spruce is somewhat less in the north than the south, the length of life is about the same. Consequently, spruce is generally taller in the south and each stand includes some trees which are larger than the largest in the north. In spite of this, virgin stands in either area would include trees of about the same maximum age with few solid trees older than 300 years.

The life-expectancy of both firs is much less than that of the spruce. Perhaps 150 years is a fair estimate of average maximum age. Several trees, under apparently favorable conditions, were found to have died at about 125 years although their size (over 20 inches) indicated they had grown well. The oldest accurate count for Fraser fir was 168 years (15.3 in. DBH) and for balsam fir, 148 years (12.5 in. DBH). All stands typically had much down-timber in all degrees of decomposition and scattered dead standing trees which, of course, indicates a constant thinning out of over-mature individuals as is typical of virgin climax stands.

Evidence is inadequate for discussing the birches more than to suggest that they live as long or longer than the firs. One of the oldest borings obtained was for 180 years on a yellow birch which was 21.4 inches DBH.

A point of possible additional interest is that all of these climax species require some 40 years to attain sapling or transgressive size (about 7 feet tall or more than 1 inch DBH).

Shrubs.—Total density of the six shrubs in the south is slightly higher than that of the four shrubs tallied in the north and the average frequency per species is also somewhat greater. The relative abundance of Sorbus in the north is balanced by the numbers of *Vaccinium erythrocarpum,* restricted to the south and the most abundant shrub there. Note that *Viburnum alnifolium* occurs with about equal numbers in both areas and with a consistently high and similar distribution. This is true of none of the other shrubs.

TABLE VII. *Average cover and frequency of herbs in southern and northern stands*

	Average cover %		Average frequency	
	South	North	South	North
Oxalis montana	52(25–65)	19(0–35)	100	55
Dryopteris dilatata	29(.5–59)	3.2(0–6)	52	30
Aster acuminatus	1.2(.5–3.9)	0.4(0–1.5)	26	20
Clintonia borealis	0.9(0–4.9)	2.5(.2–4.7)	13	45
Senecio rugelia	5.5(0–15.9)		26	
Cornus canadensis		3.9(0–8.4)		30
Aver.	23.6	11.3	52.7	46.7

Herbs.—Data for cover and frequency were obtained for all herbs but little would be gained by presenting them in complete form. Characteristic and constant species have already been described and species of lesser significance must, of necessity, have relatively low values. A few species are so characteristically conspicuous that it seems advisable to give the data to indicate their degree of dominance in the herb stratum (table 7).

Perhaps the Oxalis and Dryopteris are the best indicators but, in the rare instances where both might be absent or inconspicuous, the combination of the other species would surely mark the type of forest here considered. The total herb cover is substantially greater in the south than in the north but the general aspect is much the same especially when taken in conjunction with the ubiquitous bryophyte cover. At the same time the characteristically southern and northern species make for a clear distinction.

DISCUSSION

Forests dominated by one or more species of Picea and Abies are widely distributed through the northern half of North America. This great vegetational complex of the boreal forest is characterized throughout much of its transcontinental range and southward along the principal mountain systems by various combinations of species of the two genera. It is not the purpose of the present paper

to go thoroughly into the structure of this climax complex. However, data on comparative structure of the Appalachian representation of the spruce-fir forest can serve as a start in an analysis of the structure and developmental history of the whole North American boreal forest.

The major variations of the boreal forest are reasonably well known from a general descriptive standpoint. However, sociological analyses of individual stands representative of the different variations are almost totally lacking. Most of the detailed phytosociological work on virgin forest in North America is concerned with the deciduous forest or the mixed forests of conifers and deciduous species occurring between the deciduous forest and the true boreal spruce-fir climax. Jones (1945) in his survey of the north temperate virgin forest has commented on the relative lack of detailed studies on the North American "arctic forest" but indicates that because of its simpler structure, as compared with the forests to the south of it, the general nature of the forest seems fairly clear. Certainly many more quantitative studies are needed before the comparative structure within this large climax is sufficiently clear.

Undoubtedly the best quantitative information on the main body of the boreal forest is to be found in the classic work of Cooper (1913) on the *Abies balsamea-Picea glauca-Betula papyrifera* forest of Isle Royale in Lake Superior. Cooper was also probably one of the first to point out the similarity between the main boreal forest which he studied and that of the high summits of the southern Appalachians for which he used the data of Harshberger (1903). In recent years, Cain (1935) and Brown (1941) have published quantitative phytosociological data on virgin spruce-fir forest in certain areas of the southern Appalachians. Up to the present time, these seem to be the only studies on virgin spruce-fir using modern analytical methods.

From the present comparative studies, it is clear that in spite of the Pennsylvanian gap, the spruce-fir forests of the northern and southern parts of the Appalachian system are quite similar. The two forests were undoubtedly connected during the Pleistocene when much of the surrounding lowland was also covered by spruce, fir, and other northern species (Brown 1938; Potzger and Otto 1943; Cain 1944a, 1944b; Potzger 1945; Buell 1945, 1946; Davis 1946; Potzger and Tharp 1947). Even in those times, the montane spruce-fir of *Picea rubens* and *Abies fraseri* may have been somewhat different in composition from the surrounding lowland boreal forest since Brown (1938) reports macrofossils of *Picea glauca* and *Thuja occidentalis* from Louisiana, and Potzger and Tharp (1947) identify *Picea glauca, P. mariana,* and Abies pollen in a deep bog in south central Texas. During the cooler periods of the Pleistocene, the forests of much of southeastern North America may have resembled the present situation in northern New England (Harvey 1903; Harshberger 1905; Adams *et al.* 1920; Moore and Taylor 1927) with a red spruce-fir forest confined largely to the mountains and surrounded by a forest dominated by fir and hardwoods with black spruce and white spruce in the colder lowland bogs and also near timberline.

As the climate ameliorated, the lowland spruce, fir, and northern hardwoods gave way to deciduous forests of the more temperate types whose ranges were expanding northward. The montane spruce-fir moved northward along the mountains and upward in the southern ranges which had sufficient altitude to provide a suitably damp and cold climate. In the middle Appalachians where the mountains are too low for this climate, other forests occupied even the summits of the ranges, thus separating the Appalachian boreal forest into two divisions. Many of the dependent plants and animals found suitable environments on both sides of the gap and now exhibit disjunct distributions. Others, particularly in the south, have been isolated sufficiently long and

seem plastic enough genetically to have developed different characteristics from their northern and more widespread counterparts.

More quantitative information appears to be available for the southern Appalachian spruce-fir type than for any other region in the boreal forest. It is quite distinct and its boundaries are fairly well known (Core 1929; Davis 1930; Korstian 1943). While the present study indicates a high degree of similarity between the northern and southern Appalachian spruce-fir types, the areal extent and northern boundaries of the northern type are difficult to determine. This is because of the inclusion in the north of several widely distributed species such as *Betula papyrifera* and *Abies balsamea* which are important in the boreal forest far to the north and west. Still there seems to be justification for the more or less arbitrary delimitation of an Appalachian spruce-fir segregate even in the north on the basis of the dominance of *Picea rubens*. While this species does grow almost down to sea-level in the northern part of its range, it is primarily a montane species growing in a spruce-fir forest that appears relatively luxuriant and more like the southern Appalachian type than it does the southern fringes of the true boreal forest bordering it on the north. This north-south resemblance within an eastern or Appalachian subdivision of the spruce-fir boreal forest has been shown for birds also by Stewart and Aldrich (1949). They have found that the nesting bird population in a red spruce forest in West Virginia is more like that of a red and white spruce forest on the coast of Maine than either is like that of a spruce-fir forest in western Ontario.

While it seems possible to distinguish an Appalachian variant of the northern spruce-fir forest, it becomes difficult to separate the two in their region of overlap in southeastern Canada. Here, the presence of the closely related *Picea mariana* and *P. glauca* tends to obscure the importance of the red spruce and the montane forest merges imperceptibly into the main body of the boreal forest. A great deal more work is needed in that particular region on the relative distributions and habitat tolerances of the three eastern spruces and other critical species before any final statements can be made concerning the northern limits of a truly Appalachian spruce-fir forest. It is to be hoped that through such detailed work on the ecology of the dominants and through continued phytosociological analyses of virgin stands, the relationships between the boreal forest and its various montane extensions will be made more clear.

Summary

1. The objective of this study was (a) to record the composition and structure of representative virgin spruce-fir stands in the Appalachian mountains as part of a larger study of boreal coniferous forest and (b) to determine by comparison, the relationship of the southern Appalachian stands to those of the north.

2. Using phytosociological methods nine virgin stands in the Great Smoky Mountains and four in the White Mountains were studied intensively to obtain data for north-south comparisons.

3. Limited climatological data show that, at the greater altitudes of the zone in the south, conditions are not too different from those in the north. However, temperature extremes are not as great in the south, humidity and precipitation are consistently higher, and less precipitation is in the form of snow. Soils in both areas are podzols but the profiles in the north regularly have thicker and more distinct organic horizons.

4. Presence lists show a similarity and a distinctness in the northern and southern forests. Among the trees, shrubs, herbs, and bryophytes there are species which occur in both the north and south with high presence values and some found only in the south, others only in the north.

An unusually high proportion of species are constantly present.

5. Cover-stratification diagrams show a greater average height of trees and substantially more cover for herbs and bryophytes in the south. Density-basal area data as well as phytographs show that spruce and fir are the major species in this forest with yellow birch next in importance in the south and paper birch in the north. Fir trees tend to be present in greater numbers than spruce but the latter always has a greater total basal area. Above 10 inches DBH spruce trees are always more abundant than fir.

6. All evidence indicates that growing conditions for spruce and fir are more favorable in the south but both firs grow more rapidly than the spruce. Most stands include some spruce at least 300 years old but the average maximum age of fir is nearer 150 years. Dead standing and down trees are numerous in all stands as is characteristic of virgin climax forest.

7. Quantitative data combined with presence values show that a few shrubs and herbs in several possible combinations are regular associates of the community and may be taken as its indicators.

8. On the basis of physiognomy and composition it is maintained that the spruce-fir forest of the Appalachian is distinct but yet a part of the boreal forest formation. Floristic and ecological differences in the north and south are such that two phases should be recognized: red spruce-Fraser fir and red spruce-balsam fir.

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THE OCCURRENCE OF ORTHOPTERA AT HIGH ALTITUDES, WITH SPECIAL REFERENCE TO COLORADO ACRIDIDAE [1]

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Among the most abundant animals at high altitudes are the grasshoppers. In the alpine zone of the Colorado Rockies these apparently exceed all other kinds of insects—in numbers of individuals if not in numbers of species. The statement that insects of complete metamorphosis predominate at high altitudes, whereas the "warmth-loving" Orthoptera are less well adapted to the cold of such regions (Hesse 1924; Erhard 1931), seems to be based on observations of conspicuous rather than abundant forms. The butterflies and beetles of high altitudes are perhaps better known than are the Orthoptera, as suggested by the summary of Holdhaus (1929), and the butterflies are certainly more conspicuous. Furthermore, more species of Coleoptera and Lepidoptera than of Orthoptera undoubtedly do occur at high altitudes, but the same relationship holds at low altitudes. On the other hand, if we consider numbers of individuals, disregarding numbers of species, we may safely say that grasshoppers are often the predominant insects at high altitudes, just as stated by Prenant (1933). They are certainly among the most significant ecological units of the alpine zone.

There seems to be no a priori reason for the statement that insects with complete metamorphosis are poorly adapted to the cold of high altitudes. The statement is not supported by the known facts of distribution. In the Alps, Collembola occur at higher altitudes than any other insects (Erhard 1931). Hemiptera as well as Orthoptera occur in considerable numbers in alpine regions. Some primitive insects are actually dependent upon cold for survival. *Grylloblatta,* for example, cannot long survive at temperatures above approximately 60° F. (Walker, 1937), and its optimum temperature seems to be close to 39° F. (Mills and Pepper 1937). One of the Acrididae, an unnamed species from Mount Everest, appears to hold the high altitude record for an established insect species. Major Hingston (1925), who made observations on natural history while a member of the 1924 Everest Expedition, found early nymphs of a grasshopper at 18,000 feet above sea level, the limit of vegetation. Uvarov (1925) was unable to name these and stated that they were representatives of an undescribed species. In the same paper, Uvarov described a new genus of wingless grasshoppers, *Dysanema.* Appropriately enough, he named the two new species in this genus *irvinei* and *malloryi* after A. C. Irvine and G. Mallory, the two members of the Expedition who lost their lives in the final assault on the summit. The two species of grasshoppers occurred at altitudes of 15,000 and 16,000 feet on Mount Everest. Where vegetation occurs at such altitudes in any part of the world we may reasonably expect to find Orthoptera. Altitude, as such, is not a barrier.

Orthoptera have been recorded from alpine regions all over the world. Good general summaries of their occurrence have been given by Scudder (1898), Chopard (1928), and Uvarov (1928). In addition, some discussion of their occurrence has been combined with the excellent general accounts of alpine animal ecology by Hesse (1924) and Erhard (1931).

Most of the records of high altitude occurrence are, of course, scattered through taxonomic accounts of collections made in mountainous regions. Unfortunately, the importance of complete data —even with reference to altitude alone—

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was not recognized by early collectors, localities being designated by such vague expressions as Tibet, Colombia, or Rocky Mountains. The information on high altitude Orthoptera is naturally more complete from the mountains of Europe and North America than elsewhere. We were particularly fortunate in the United States in that the first great student of Orthoptera in this country, Samuel H. Scudder, was an ardent mountain climber. Limited collections, however, and individual variations led to an early multiplicity of names that seems more complex than in the taxonomy of lowland species. Mountain climbing is strenuous, too, and the accumulation of representative collections from scattered alpine areas is a long-time process.

Types of Orthoptera Represented

Not all groups of Orthoptera are well represented at high altitudes. Some, however, appear to be particularly well adapted to the cold conditions of the alpine zone. The Grylloblattidae, for example, are associated in general with cold, damp situations. They have been found in the mountains of western Canada and northwestern United States, among rocks at the edge of snow-fields, in areas covered with snow much of the year. Some of the Tetrigidae, likewise, are tolerant of cold, damp situations, and occur in the alpine zone.

Species which are quite active at night, as are many Gryllidae and Tettigoniidae, are absent from alpine regions. Nor are they likely to occur even as accidental visitors, because wind movements in mountains are usually downward at night. Crickets appear to be absent from high altitudes, at least in the Holarctic Region. The diurnal Tettigoniidae, however, are represented by several high altitude species, in the Old World as well as in the New. In this country we have several species thoroughly adapted to alpine conditions. *Anabrus simplex* Haldeman, the Mormon "cricket," completes its life cycle in Colorado at altitudes up to 13,000 feet above sea level (at least as far north as Mount Evans). *Acrodectes philopagus* Rehn and Hebard, another decticine, was described from specimens collected near and at the summit of Mount Whitney (California), 14,500 feet, the highest mountain in the United States (Rehn and Hebard 1920). One of the cave-crickets, *Ceuthophilus alpinus* Scudder, was collected above timber line on Mount Lincoln, in Colorado (Scudder 1898). All of the forms just mentioned are flightless; wings, if present, are much abbreviated.

The majority of the alpine Orthoptera, some of which have wings of normal length, are members of the family Acrididae. Undoubtedly, hundreds of species in this family will eventually be known from the alpine regions of the world, where they occur as well-adapted resident insects. The activity of the American species with which I am familiar, at air temperatures below 50° F., is convincing evidence of efficient physiological adaptation to cold temperatures. The high altitude species are obviously better adapted to cold than are those of low altitudes, even when closely related taxonomically.

Ecological Categories of High Altitude Species

When a flightless insect as large as the average decticine (or even a small grasshopper, for that matter) is found regularly at a given altitude we may consider this reliable evidence that it is established at such an altitude, i.e., that it is able to complete its life cycle at that altitude. On the other hand, among the numerous species of fully-winged grasshoppers recorded from alpine regions we must distinguish carefully between those that are native to the altitudes in question and those that are accidental or casual in occurrence. Since grasshoppers are primarily diurnal in activity, and since diurnal air movements in mountainous regions are predominantly upward, we find that a large number of species at high altitudes are accidental. A combination of flight ability, which need not be great, and favor-

able wind currents is undoubtedly responsible for the arrival of such accidental visitors. The possibilities of passive dispersal of this sort have been summarized by Holdhaus (1929). In commenting upon the same phenomenon, Chopard (1938) has pointed out that this high degree of vagility is not necessarily accompanied by a high per cent of establishment in new areas. In other words, we are apparently dealing with species that annually repeat on a large scale their invasions of the alpine region, but which, lacking the necessary preadaptation, have not yet become established there. Several of the species attributed to the alpine zone in Colorado, in particular *Melanoplus mexicanus mexicanus*[2] and *Melanoplus occidentalis,* are apparently in this category. It is important, therefore, to know something of the life histories of long-winged species that occur at high altitudes. Without this information it is not possible to determine whether a species is present as a resident or merely as an accidental visitor.

In the ecological classification suggested by Hesse (1924), three types of alpine animals are recognized, eualpine, tychoalpine, and xenoalpine. Belonging to the first category are those that are exclusively alpine; to the second belong those that extend into the alpine zone from below and are able to complete their life cycles in the higher zone; in the third group are those that invade the alpine zone but are unable to establish themselves there.

This classification was devised for the fauna of the Alps, a mountain mass isolated from northern regions by intervening lowlands. It is not appropriate in the Rocky Mountains, however, for in the Rockies the populations of alpine species in southern latitudes are in more or less continuous geographic contact with populations of the same or closely related species at lower altitudes to the north. There are no eualpine species in the meaning of Hesse's term; a species which appears to be eualpine in the southern part of its range may not be alpine at all farther north. All our characteristic alpine species would be considered tychoalpine according to Hesse's classification. This, however, implies that they are related to species of the adjacent lowlands, whereas their affinities are with low altitude species which occur farther north. Xenoalpine or accidental species do occur in numbers, however, and these undoubtedly occur in mountains of all regions.

A satisfactory ecological classification of the alpine fauna of the Rocky Mountains appears to require only two categories. We must distinguish between species which can complete their life cycles in the alpine zone and those that reach the zone but cannot become established at that altitude. The former are characteristic of the zone; they are here designated "resident alpines." The numerous species which invade the alpine region from below but cannot become established are the "accidental alpines."

High Altitude Grasshoppers in Colorado

Since the summer of 1931 I have been interested in the altitudinal distribution of Colorado grasshoppers. Collections at altitudes from the plains (5,000 feet) to over 13,000 feet above sea level have been made in northern Colorado throughout this period. These collections were chiefly in the Boulder region, but occasional trips have been made into the mountains of other parts of the state. Personal observations were supplemented during the season of 1949 by extensive collections made by H. A. Fehlmann, graduate student at the University of Colorado, in the alpine zone of the Culebra, Sangre de Cristo, and Mosquito Ranges. Published records have been used to supplement personal observations and those of Mr. Fehlmann. In spite of the apparent extensive coverage, however, there are still large areas of alpine country in Colorado where grasshoppers have not been collected.

[2] Author names of Colorado Acrididae are given only in the list near the end of the paper.

The present report is limited to a discussion of grasshoppers (Acrididae) of the alpine zone. This is the mountain zone which occurs above timber line. Timber line in Colorado is at an altitude of about 11,000 feet in the northern part of the state, at about 12,000 feet in the Culebra Range and other mountains of southern Colorado. The Acrididae referred to are all listed in the last section of this paper, preceding the Summary.

A geographic study of the distribution of species waits upon additional collections and taxonomic reexamination of some of the high altitude groups. Large series covering the entire range of each species should be collected. Meanwhile, the recognition of the ecological category to which each species thus far collected belongs may prove of value.

The method of recognizing a winged species as a resident alpine is relatively simple if local life history studies are available. If a species is collected above timber line in the adult condition, and the flightless nymphs of the same species are found in the same locality, it is considered characteristic of the alpine zone. If, on the other hand, an adult grasshopper is collected above timber line without juveniles of the same species we must ask its source. If one knows from observations at lower altitudes that it is just appearing as an adult some five thousand feet lower down the assumption is clear that it has been transported upward. If we follow this species through the season at different altitudes we are able to determine its maximum range of altitude as a resident. If it occurs anywhere above that range it is accidental.

The special case of *Melanoplus mexicanus mexicanus* is highly informative, particularly since it has been referred to as an alpine form on the basis of adult specimens alone (Hebard 1935, 1936). The species is highly vagile, and has repeatedly been taken in numbers above timber line. One striking observation illustrates the real nature of this occurrence. On July 18, 1948, I found numerous adults of this species frozen in the surface of a snow bank at about 12,200 feet altitude on the east side of Mount Audubon (Colorado). These grasshoppers had fallen on the snow not many hours or days before, because the snow bank had not yet receded to its size in the preceding autumn. The alpine species in the adjacent area were still juveniles, not having reached the adult condition, while *M. m. mexicanus* was already a common adult on the plains seventeen miles due east and seven thousand feet lower down. The adults in the snow bank had undoubtedly flown or been carried on rising air currents to the high altitude.

A more complete demonstration is afforded by the record of collections during 1949, as these collections were made to determine the time of development at different altitudes. Early juveniles of *M. m. mexicanus* were collected on the plains and as high as 7,600 feet by the last of May, and these were adult by the first of July. Juveniles were taken as early as the third week in June at 8,500 feet, but the first adults did not mature at that altitude until about the first week of August. The highest elevation at which juveniles were collected was 9,800 feet. Juveniles appeared there as early as the first of August, but the first adults associated with last instar nymphs were not collected until after the first of September. As late as October 1, juveniles and adults were both still present at 9,800 feet, but cold weather had already set in at that altitude. Meanwhile, on September 8, an adult female of this species was collected by H. A. Fehlmann at an altitude of 12,300 feet on Mount Evans. This grasshopper may have come all the way from the plains; in any case it must have originated from an altitude at least 2,500 feet lower than that at which it was collected.

Other high altitude records of this species in Colorado give additional evidence that *M. m. mexicanus* is not typical of the alpine zone. On July 13, 1936, an adult male and three adult females were

collected above timber line, at 11,400 feet, on Niwot Ridge (near Science Lodge, University of Colorado mountain laboratory). On July 20, the same year, three males and eight females, all adults, were collected above timber line on Mount Audubon, one of the females being collected on the cold rocks of the windblown summit, at 13,300 feet above sea level. H. A. Fehlmann collected adults during August 1949, from alpine areas above 12,000 feet on Trinchera Peak (Culebra Range), Greenhorn Mountain, West Spanish Peak, Sierra Blanca, Pike's Peak, and in the Mosquito Range west of Alma, Colorado. On Greenhorn Mountain, which is quite close to the plains southwest of Pueblo, thirteen adults were taken above 12,000 feet on August 3 and twenty-six on August 25. No juveniles were collected in any of these alpine areas, nor have I found any records of juveniles taken above timber line in this region. Furthermore, we do know that *M. m. mexicanus* is capable of flying or being carried many miles (Munro and Sangstad (1938). The evidence seems clear that it is an accidental alpine.

The evidence with reference to *Melanoplus occidentalis* is not so clear. It has been found above timber line on numerous occasions, and was listed by Hebard (1929, 1935, 1936) as an alpine species in Colorado and New Mexico. On July 13, 1936, I collected eight males and two females, all adult, above timber line on Niwot Ridge. A single adult male was collected by Robert J. Niedrach on August 10, 1933 at 13,600 feet on Mount Evans. I have no records, however, of juveniles above timber line, nor have I seen such records in the literature. Furthermore, the species is highly vagile (La Rivers 1948). The evidence available thus far points, therefore, to recognition of this species as a purely accidental alpine grasshopper, which is not established above timber line.

Other species occasionally listed as alpine in distribution include *Melanoplus bivittatus* and *Melanoplus femur-rubrum*. The former completes its life cycle up to about 9,500 feet, but juveniles are scarce at that altitude. *M. femur-rubrum* apparently does not occur much above 8,000 feet in the juvenile condition. Both these species are collected not infrequently above timber line, where they are of course accidental.

Arphia conspersa, since of boreal affinities, is a species that we might expect to find established in the alpine zone. Adults are found above timber line (Hebard 1929), but in the Boulder region I have not collected juveniles above approximately 9,800 feet. In favorable spots this species may be able to complete its life cycle above timber line, but at present I am inclined to consider its occurrence at such altitudes accidental.

Another one of the Oedipodinae listed by Hebard (1929) as alpine in Colorado is *Camnula pellucida,* but Hebard failed to list any alpine collecting localities. I have not collected this species above timber line but have taken both juveniles and adults from 6,000 to 10,000 feet. In favorable areas this species may be able to complete its life cycle above timber line. It should not at present be considered alpine, however.

One other macropterous species of uncertain status, *Chorthippus longicornis,* may upon further collecting prove to be a resident alpine. Adults have been taken above timber line, but this species is so highly restricted in habitat that a special search will have to be made at the right time and place before we can be sure that it does complete its life cycle above timber line. It does complete its life cycle in wet patches of sedges up to about 10,500 feet in the Boulder region, and my son and I have collected juveniles and adults on Hoosier Pass (11,500 feet), just at timber line.

One of the interesting aspects of the occurrence of accidental species above timber line is the observation that at certain times, apparently during quite warm weather, abnormally large numbers of these may be taken in a single day. I

have previously referred twice to collections made July 13, 1936 on Niwot Ridge, near Science Lodge. Niwot Ridge, which at its eastern end extends only a few hundred feet above timber line, carries the tundra farther east than at any other place in northern Colorado. It is an alpine ridge extending in an east-west direction, its eastern end less than fourteen miles from the plains. On the day mentioned there occurred the most extensive invasion of the alpine tundra by lowland species of which I have record. The collection above timber line on that date included adults of the following species: *Aulocara elliotti* (4 males, 11 females); *Aeropedellus clavatus* (1 male); *Amphitornus coloradus* (1 male, 1 female); *Metator pardalinus* (2 males, 1 female); *Melanoplus bivittatus* (8 males, 2 females); *M. mexicanus mexicanus* (1 male, 3 females); *M. dodgei dodgei* (5 males, 2 females); *M. occidentalis* (8 males, 2 females); *M. packardii* (2 males, 3 females); *Hesperotettix viridis viridis* (1 female). Two of these species were typical alpines, *Aeropedellus clavatus* and *Melanoplus dodgei dodgei.* Eight juveniles of the former and seven of the latter were collected. On the other hand, no juvenile specimens of any of the other eight species were collected. They were all accidentals.

Among the observations made during the summer of 1949 by H. A. Fehlmann, at least one such unusual collection was noted. One or two accidental species were collected at almost every alpine collecting locality, but the most striking collection was made on Sierra Blanca, at 12,800 to 13,000 feet, on August 24, 1949. On that date adults of the following accidentally occurring species were collected: *Dissosteira carolina* (2 males, 2 females); *Melanoplus femur-rubrum* (5 males, 6 females); *M. mexicanus mexicanus* (1 male); *M. packardii* (1 male). Juveniles as well as adults of three resident alpine species were collected. These were *Aeropedellus clavatus, Melanoplus dodgei bohemani,* and *M. borealis monticola.* What weather conditions are associated with these invasions of high altitudes by lowland species we do not know, but the invasions are necessarily associated with rising air currents.

Among the grasshoppers with fully developed wings at least three species in the front range of the Colorado Rockies are resident alpines. These are: *Melanoplus alpinus,* of the northern Colorado mountains; *M. borealis monticola,* of the mountains of southern Colorado; and *Xanthippus corallipes altivolus,* with a wider north-south range than either of the other two species. The last of these forms has somewhat reduced wings, those of the female occasionally being too short to support sustained flight, but both species of *Melanoplus* have moderately long wings. I have collected many juveniles of *M. alpinus* and *X. c. altivolus* in the alpine zone in the mountains west of Boulder, Colorado. With H. A. Fehlmann I collected juveniles of *M. b. monticola* in the Culebra Range in July 1949, and during August of the same season he collected both juveniles and adults of this species on Greenhorn Mountain, on Sierra Blanca, in the northern Sangre de Cristo Mountains, and as far north as Pike's Peak. These three species are the only fully winged grasshoppers normally present in the alpine zone along the eastern range of the Rockies in Colorado.

A fourth macropterous form, *Melanoplus bruneri,* appears in the alpine zone of mountains in the central part of the state. This was recorded from an "alpine environment" near Gothic by Hebard (1929), two adult males and a juvenile female having been collected by Mary J. Brown. Under the name *Melanoplus excelsus* it was recorded from above timber line on Mount Lincoln by Scudder (1898).

Melanoplus borealis stupefactus is a brachypterous subspecies of *M. borealis* that occurs in the alpine zone of New Mexico and in the mountains west of the San Luis Valley and as far north as Gothic (Hebard 1935). I find no definite record of its occurrence above timber line

in Colorado, but there is a questionable record mentioned by Scudder (1898) under the name *Podisma stupefacta.*

The majority of the resident alpine species in Colorado are short-winged. *Aeropedellus clavatus,* of wide latitudinal range, appears to have the widest altitudinal range of any alpine species, completing its life cycle in the Boulder region at all altitudes from 5,500 to 13,500 feet. The short-winged *Melanoplus dodgei* complex, for which I use the nomenclature of Hebard's Colorado paper (1929), is represented by the small alpine subspecies in northern Colorado (*M. d. dodgei*) and a larger subspecies (*M. d. bohemani*) above timber line in the southern mountains of the state. Hebard, in a later paper (1935), recognized *bohemani* as a distinct species. I have retained the earlier name, however, as it indicates what appears to me to be a close relationship with *M. d. dodgei.*

Melanoplus oregonensis marshallii is another brachypterous form, its tegmina and wings being shorter even than those of *M. dodgei.* It occurs in alpine communities in the Mosquito Range and as far north as Loveland Pass. It occurs north of Loveland Pass below timber line. *Melanoplus kennicotti nubicola,* which has been recorded from a few alpine areas in the central part of the state, is unquestionably alpine, but its geographic distribution is not yet well understood.

I have collected juvenile and adult *Melanoplus fasciatus* a short distance above timber line in the Boulder region, and, for that reason, have listed the species as a resident alpine. However, it is possible that it should be considered accidental on the tundra in spite of the fact that it is relatively short-winged. It is ecologically associated with the forested portions of the mountains, and is able to complete its life cycle up to and within the dwarf forest at timber line. Even juveniles, at least in the later instars, could hop the short distance from the forest to the tundra areas where they have been collected.

In any particular alpine area of the front range the community of resident alpine grasshoppers appears to include not more than three species at the same time. *Xanthippus corallipes altivolus* is the only species that over-winters in the juvenile condition above timber line, and, consequently, it is the only species that becomes adult before mid-summer. In the latitude of Boulder, adults mature at 11,000 feet as early as the last week of June. By the middle of July, *Aeropedellus clavatus* and *Melanoplus dodgei* are adult. Both of the macropterous melanopli, *M. alpinus* and *M. borealis,* become adult toward the end of the season, about the middle of August, but while *A. clavatus* and *M. dodgei* are still present. Adults of Xanthippus have disappeared by that time, though juveniles hatch as early as the last of August from eggs laid the same season. Since the two macropterous melanopli do not occur in the same locality, the usual combination of species is: *A. clavatus, M. dodgei,* and either *M. alpinus* (in the north) or *M. borealis* (in the south). Neither of the last two species is necessarily present, however. If *Melanoplus oregonensis marshallii* is present, *M. dodgei* appears to be absent. Thus we have as the typical alpine grasshopper population the wide-spread *A. clavatus,* a short-winged species of *Melanoplus,* and a long-winged species of *Melanoplus,* all of these following an early season form, the over-wintering *Xanthippus corallipes altivolus.*

Colorado Acrididae Collected in the Alpine Zone

The following is a list of all species of Acrididae known from above timber line in Colorado. Most of these have been collected by the writer. Some were collected by H. A. Fehlmann in his 1949 expedition. If the only records available are his, the names are followed by the initials H. A. F. in parentheses. Some names are based on published records only. The sources for these are indicated by reference to the literature list, likewise in parentheses following the names.

Those Acrididae that are resident alpine species, completing their life cycles above timber line, are indicated by an asterisk preceding the name. Species not so marked are considered of accidental occurrence.

Acridinae:
- **Aeropedellus clavatus* (Thomas)
- *Ageneotettix deorum* (Scudder)
- *Amphitornus coloradus* (Thomas)
- *Aulocara elliotti* (Thomas)
- *Chorthippus longicornis* (Latreille) (May be a resident alpine species)

Oedipodinae:
- *Arphia conspersa* Scudder (Hebard 1929)
- *Circotettix rabula altior* Rehn
- *Dissosteira carolina* (Linnaeus) (H. A. F. collection)
- *Metator pardalinus* (Saussure)
- *Sphaʀagemon collare* (Scudder)
- *Trachyrhachis kiowa* (Thomas)
- **Xanthippus corallipes altivolus* (Scudder)

Cyrtacanthacrinae:
- *Hesperotettix viridis viridis* (Thomas)
- **Melanoplus alpinus* Scudder
- *M. bivittatus* (Say)
- **M. borealis monticola* Scudder
- *M. borealis stupefactus* (Scudder) (Scudder 1898; questionable)
- **M. bruneri* Scudder
- **M. dodgei dodgei* (Thomas)
- **M. dodgei bohemani* (Stål)
- **M. fasciatus* (F. Walker) (May be accidental)
- *M. femur-rubrum* (DeGeer) (H. A. F. collection)
- **M. kennicotti nubicola* (Scudder) (Scudder 1898, as *Podisma nubicola*)
- *M. mexicanus mexicanus* (Saussure)
- **M. mexicanus spretus* (Walsh) (Extinct; juveniles reported by Scudder 1898)
- *M. occidentalis* (Thomas)
- **M. oregonensis marshallii* (Thomas)
- *M. packardii* Scudder

It should be noted that of the total number of twenty-eight species and subspecies collected above timber line in Colorado only eleven (approximately 39%) may be considered characteristically alpine in distribution, and one of these (*Melanoplus mexicanus spretus*) is now extinct.

Summary

1. Orthoptera of several families occur at high altitudes. The Acrididae are represented by the largest number of species. In numbers of individuals they are among the most numerous insects at high altitudes. Their abundance leads one to question the statement that insects with complete metamorphosis are better adapted to alpine climatic conditions than are those with incomplete metamorphosis.

2. High altitude Orthoptera of the Rocky Mountains of Colorado are of two ecological groups, resident alpines and accidental alpines. The former can complete their life cycles above timber line. Accidental alpines occur in the alpine zone only as adults, flying or being borne to the alpine areas on air currents. The majority of species of Acrididae recorded from alpine areas of Colorado are accidentals. Only eleven (approximately 39%) of the twenty-eight recorded species and subspecies are resident alpines.

3. *Melanoplus mexicanus mexicanus, M. occidentalis,* and several other species previously recorded as alpine grasshoppers are not resident species but accidental visitors. The resident alpine species of Colorado are: *Aeropedellus clavatus, Xanthippus corallipes altivolus, Melanoplus alpinus, M. borealis monticola, M. bruneri, M. dodgei dodgei, M. dodgei bohemani, M. fasciatus* (may be accidental), *M. kennicotti nubicola, M. mexicanus spretus* (now extinct), *M. oregonensis marshallii.* None of these is confined, except locally, to the alpine zone.

4. In any given alpine area along the eastern ridge of the Colorado Rockies the grasshopper population may include an early summer species which over-winters as a juvenile (*Xanthippus corallipes altivolus*), *Aeropedellus clavatus* and a short-

winged *Melanoplus* in mid-summer, and a long-winged *Melanoplus* in late summer. Apparently two species of brachypterous melanopli or two species of macropterous melanopli do not occur at the same time and place.

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SPAWNING AND SETTING OF THE AMERICAN OYSTER, *O. VIRGINICA,* IN RELATION TO LUNAR PHASES

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Introduction and Review of Literature

A revival of interest in the relation between the lunar phases and periodicity in the breeding of marine animals has been recently stimulated by Korringa's (1947) article. Although his article is chiefly devoted to a review of the literature on this subject and its analysis, the author, nevertheless, incorporates in it his own observations on the periodicity of swarming of the larvae of the European oyster, *Ostrea edulis,* in the Oosterschelde, Holland, during the period from 1935 until 1946. Korringa's extensive data led him to the conclusion that in his district there is a well-defined periodicity in the spawning of *O. edulis* and swarming of its larvae, and that this periodicity is directly correlated with the phases of the moon.

Korringa found that the important maxima of extrusion of the eggs (heavy spawnings) into the mantle cavity of female oysters take place at the spring tides, occurring 2 days after full and new moon. About 8 days after spawning the larvae are released from the mother's mantle chamber and appear in the water in large numbers. This phenomenon, known as swarming, happens about 10 days after full or new moon. Of course, the dates of spawning are of primary importance because swarmings follow them almost automatically. Korringa thinks that periodicity in the spawning of *O. edulis* is caused by the rhythmical differences in the water pressure occurring between the neap and spring tides. According to Korringa (1947) "it is the rhythm of the tides which does the trick."

Since an extensive review of literature on the relation between the phases of the moon and the periodicity of spawning of marine animals has already been offered by Korringa, it is not necessary to discuss it at length in our paper. We shall confine ourselves to those references that concern oysters. Orton (1926), working in Fal-Estuary, England, on *O. edulis* came to the conclusion that there was a periodicity in its spawning, the maxima occurring near full moon. He thought, however, that periodical spawning was noticed only in normal oysters, while "dumpy" or irregularly-shaped oysters showed no such rhythm. Orton suggested that the rapid rate of change in hydrostatic pressure at the spring tides accompanied by an increase in temperature acted as a stimulus to induce spawning. Later on, however, Orton (1937) wrote that his further observations showed no relation between the maxima of spawning and the full moon tides, and that he never again observed lunar periodicity in the spawning of oysters.

Spärck (1929) working on the same species in Limfjord found no lunar periodicity in its spawning. However, since the tidal changes and the changes in hydrostatic pressure in Limfjord are small, the lack of periodicity there could be ascribed to that reason.

In this country the nearest relative of *O. edulis* is *Ostrea lurida,* a larviparous species, intensively cultivated in some sections of Puget Sound. A description of the spawning, larval development and setting of this oyster has been given by Hopkins (1937). Hopkins found no lunar periodicity in the spawning and swarming of *O. lurida,* but established that spawning is a continuous process extending for a period of at least 5 months, although it is most active for approximately 6 weeks. Once spawning begins, it usually slowly increases to a maximum and then gradually diminishes.

Schaefer (1937) studied spawning and setting of Japanese oysters, *Ostrea gigas,*

introduced in Puget Sound. Spawning extended over a considerable period of time during the summer, but there was no correlation between the lunar phases and intensity of spawning. Schaefer thought, nevertheless, that he found a direct correlation between the rate of setting and "the lunar tidal period," because the modes of the curves of setting at all his three stations corresponded, in his opinion, with the periods of neap tides.

Schaefer's observations were made during one summer only. As will be shown later, the conclusions regarding the periodicity of spawning and setting of oysters may be misleading if based on a single summer of observations. Furthermore, a critical study of Schaefer's diagram fails to support his contention. For example, the largest peak of setting at one of his stations took place about August 22 during a neap tide period. However, the curve showing the intensity of setting at his second station was not only lacking a peak during the same period but actually showed a depression. The curve of his third station showed only insignificant variations in the intensity of setting between August 10 and September 17, and definitely lacked any pronounced peaks, which coincided with the neap tides.

Before proceeding with a review of the articles dealing with spawning of *Ostrea virginica* we should mention that our oyster differs in several important respects from its European relative, *O. edulis*. As a matter of fact, the anatomical and physiological differences of these two types of oysters are of such magnitude that many suggestions have been made to regard them as members of two different genera. One of the chief differences between them is that while *O. edulis* is larviparous, *O. virginica* is oviparous. *O. edulis* incubates the eggs, and later the larvae, in its mantle chamber for about 8 days before discharging them in the surrounding water. When discharged the larvae are already about 175 μ in length. The larvae lead a free-swimming life for about 8 to 10 days (temperature 18.0–19.0° C.) and then metamorphose into juvenile oysters, a process which in this country is called "setting" and in England, "spatfall" of oysters. *O. virginica*, on the other hand, discharges the eggs directly into the water. The eggs, which measure approximately 50 μ, soon develop into straight hinge larvae about 70–75 μ long. The free-swimming period is estimated by various writers to last from 7 to 30 days (Nelson 1908; Medcof 1939) depending upon ecological conditions.

Nelson (1928), while offering no observations on lunar periodicity, related the spawning of our oysters in Barnegat Bay, New Jersey, to temperature alone. Since no connection was shown between the times the spawning temperatures are reached and the phases of the moon, his observations lend no support to the theory of lunar periodicity.

Prytherch (1929) working on *O. virginica* in Milford Harbor and Long Island Sound expressed the opinion that in these waters the majority of the oysters spawned "at the end of the full moon tidal period, or eight days after the time of full moon." In other words, those spawnings took place during the neap tides, when the differences in hydrostatic pressure between high and low water are usually the smallest. He thought that the effect of the moon on the spawning of the American oyster is only indirect, and that the spawnings which occurred at the end of the full moon tidal periods took place then simply because of an increase in the water temperature at that time.

Hopkins (1931) working with the same species in Galveston Bay, Texas, wrote: "The period of greatest abundance of larvae in the water appears to have been from the middle of April to the middle of June. Since these larvae were predominantly in the straight hinge stage, or within about 3 days old presumably, the records may be considered to indicate the period of most profuse spawning." Obviously, Hopkins found no definite maxima spawnings that could be correlated

with certain phases of the moon. It should be remembered, however, that in Galveston Bay where Hopkins worked the mean range of tide is small, about 1.1 feet and, therefore, the changes in hydrostatic pressure there are insignificant.

Loosanoff and Engle (1940) reported no periodicity in the spawning of *O. virginica* in Long Island Sound or in Milford Harbor during the summer of 1937.

As can be seen, very little has been written on the spawning of *O. virginica* in relation to the lunar phases. The lack of such contributions is easily understood if it is remembered that reliable conclusions on this subject can be formed only after working in the same locality for a number of years, as Korringa did in the Oosterschelde. This, of course, is not often possible. In this country the senior author is one of the few fortunate enough to have had the opportunity to study the propagation of oysters in the same locality over a long period. His observations have been made for the last 13 years, beginning with 1937, on the oysters, *O. virginica,* of Long Island Sound and some of its tributaries. Sufficiently complete data are now available to discuss certain aspects of the spawning behavior of our oysters and compare them with those of *O. edulis.*

Collection of the data offered in this article was made possible through the help of the many workers employed during the 13 summers of investigation. To them we owe our sincere thanks. We are especially obliged to Mr. James B. Engle, former Oyster Culturist of our Laboratory, who for several summers participated in the field work, counting oyster larvae in the water samples and oyster set on the collectors.

Observations and Experiments

Accumulation of spawn in different years

Before proceeding to discuss our observations on the periodicity of spawning and setting of oysters in Long Island Sound it may be worthwhile to consider one of the factors which may have a direct bearing upon the number of larvae found in different years. Korringa (1947), in discussing the differences in the production of larvae in the Oosterschelde from year to year, concludes that it is mainly governed by the number of mother oysters. This assumption would be justified only on the condition that the quantity of spawn developed by the oysters from year to year would always be the same. This, of course, is not so, at least for *O. virginica.*

We have already reported (Loosanoff and Engle 1940) that the thickness of the gonadal layer of Long Island Sound oysters, of approximately the same age and size, varied considerably from year to year. Since the publication of that report, much additional information on such fluctuations has become available (Fig. 1). It shows, for example, that in 1937 the average pre-spawning thickness of the gonadal layer was more than twice as great as in 1946. It is clear, therefore, that the quantity of spawn produced by a given number of oysters in a certain year may equal or even exceed the quantity produced by twice that number of oysters in some other year.

Since there is no evidence that *O. edulis* of a certain size invariably produces the same quantity of spawn every year, it is possible that the fluctuations in the quantities of spawn accumulated by European oysters in different years may resemble those of our oysters. Korringa's own data seem to indicate that. For example, the largest numbers of larvae in the Oosterschelde were recorded in 1939, 1945 and 1946, presumably, because the numbers of mother oysters present on the beds during those years were also the largest (Korringa 1947). Yet, he reports no such maximum for 1938, although the number of oysters during that year was the same as in 1945 or 1946.

A comparison of the number of larvae produced in the Oosterschelde in 1937 with that of 1938 shows an even greater inconsistency. Although in 1938 the number of mother oysters was only about 17

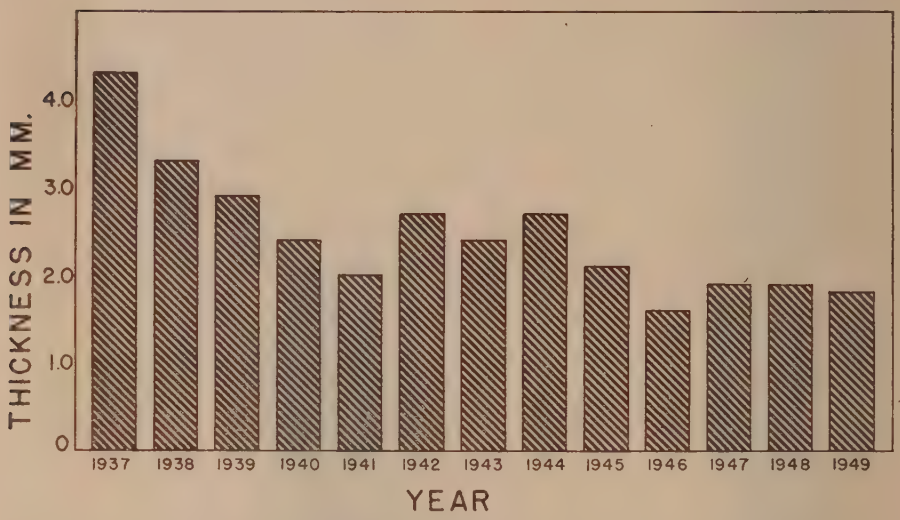

FIG. 1. Average pre-spawning thickness of gonadal layer of oysters of Long Island Sound, 1937–1949.

per cent larger than in 1937, the total production of larvae during 1938 was, according to Korringa's diagram, approximately 100 per cent greater than in 1937. Practically the same can be said in comparing the years of 1944 and 1945.

These examples are ample to show that the conception that the numbers of larvae produced in the different years should be roughly proportional to the numbers of mother oysters often does not hold true. Nevertheless, even if there is no direct ratio between the two numbers, it still should not be denied that the number of mother oysters is an important factor in governing the extent of the annual production of larvae. However, its importance varies from year to year, depending upon the physical condition of the oysters during the periods when accumulation of gonad material in their bodies is taking place, and also upon the ecological conditions which governed the accumulation of spawn. Obviously, an oyster population consisting chiefly of sick or poorly fed individuals cannot develop enough spawn to produce heavy numbers of larvae. Such is apparently the case shown by Korringa (1947) for the year 1936 when most of the oysters in the Oosterschelde were in poor condition.

To sustain further this argument it may be mentioned here that our field and laboratory observations of the past five years have shown that the quantity of spawn to be developed by oysters depends upon the quantity of glycogen and other nutritive materials stored in their bodies. Therefore, a large production of eggs can be expected only in the years when the bodies of the oysters are rich in glycogen. Since the quantity of glycogen during the pre-gonad formation period varies greatly from year to year, corresponding variations in accumulation of spawn should also be expected. This may explain why in certain years a small but healthy population can develop and discharge more spawn than a considerably larger population existing under unfavorable ecological conditions.

Occurrence and distribution of larvae

Observations of the last 13 years on the occurrence of oyster larvae in Long Island Sound showed consistently that their horizontal distribution over the oyster beds is extremely uneven. For example,

the samples collected on July 26, 1944 at five stations of the New Haven area showed the number of larvae ranging from 0 to 800 per 25 gallons of water. Because the stations were located within a short distance of each other the entire collection was completed within 1 hour and 30 minutes. The collection was repeated on July 29, August 24 and 27 of the same year and again showed extremely wide variations among the samples.

In comparing the number of larvae present on the same day in the three major districts, New Haven, Milford and Bridgeport, all of which are included in the most important part of the Long Island Sound oyster-producing area, where more than a million bushels of oysters capable of spawning are kept, the same inconsistency exists. Often when larvae were found in one district, they were almost entirely absent in the one or two others. Prytherch (1928), who also spent several summers studying the propagation of oysters in Long Island Sound, found that the abundance and distribution of larvae in the region between Bridgeport and New Haven were extremely irregular.

Because of such large differences in the number of larvae found at about the same time in different parts of the oyster-producing section of Long Island Sound and especially at closely located stations, it appears improbable that there are definite periodical maximum spawnings involving the largest part of our oyster population, such as Korringa (1947) found in the Oosterschelde. Our observations on the changes in thickness of the gonadal layer of the oysters of Long Island Sound also indicate that the discharge of spawn during the summer is quite slow and gradual without sharp decreases in the thickness that would coincide with the periods of new or full moon (Loosanoff and Engle 1942).

The absence in our waters of a definite relation between the dates of heavy spawnings and the periods of the spring tides is best illustrated by observations on the changes in the numbers of larvae at one of our stations where the samples were systematically collected during three summers. This station was located in Milford Harbor near its junction with Long Island Sound. The method consisted in pumping 25 gallons of water into

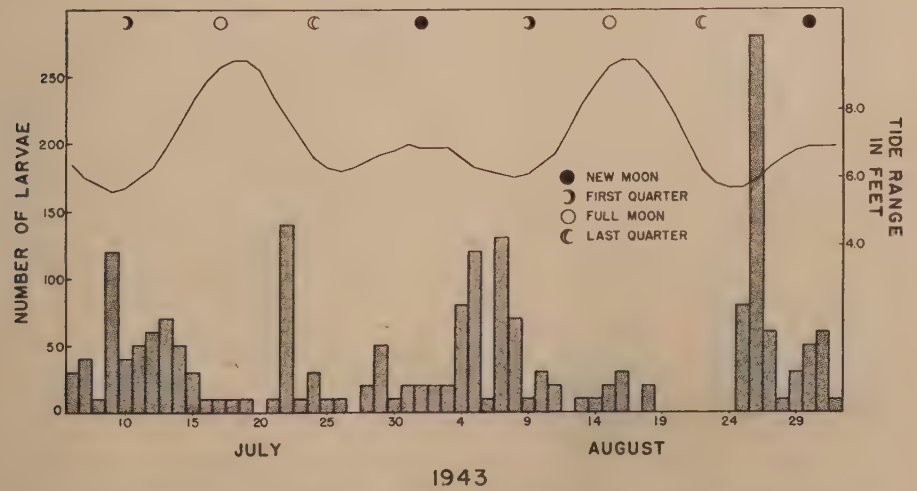

FIG. 2. Numbers of straight hinge oyster larvae per 25 gallons of water collected daily in Milford Harbor during the summer of 1943. Tide range in feet and lunar phases are also shown.

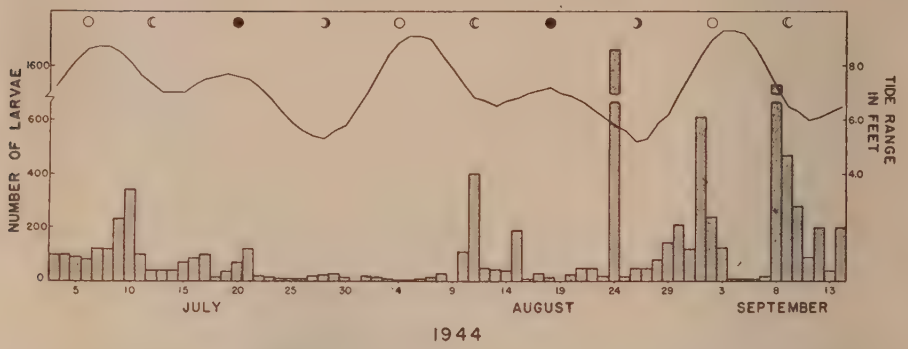

FIG. 3. Numbers of straight hinge oyster larvae per 25 gallons of water collected daily in Milford Harbor during the summer of 1944. Tide range in feet and lunar phases are also shown.

a barrel of that capacity and then filtering the collected water through a plankton net. Toward the end of the filtering the water in the barrel was strongly agitated to keep all the plankton in suspension. The samples, which were collected daily, were taken 3 feet below the surface. Counting of the larvae, a slow and tedious process when the samples were rich in plankton, was made in the usual manner using a microscope and Sedgwick-Rafter counting cell.

The samples were collected during July and August in 1943 and 1945, while in 1944 the collection was extended until the middle of September. The results of the three years of observations are given in Figures 2, 3 and 4. Only straight hinge larvae, not over 80 microns in length, thus indicating that they were developed

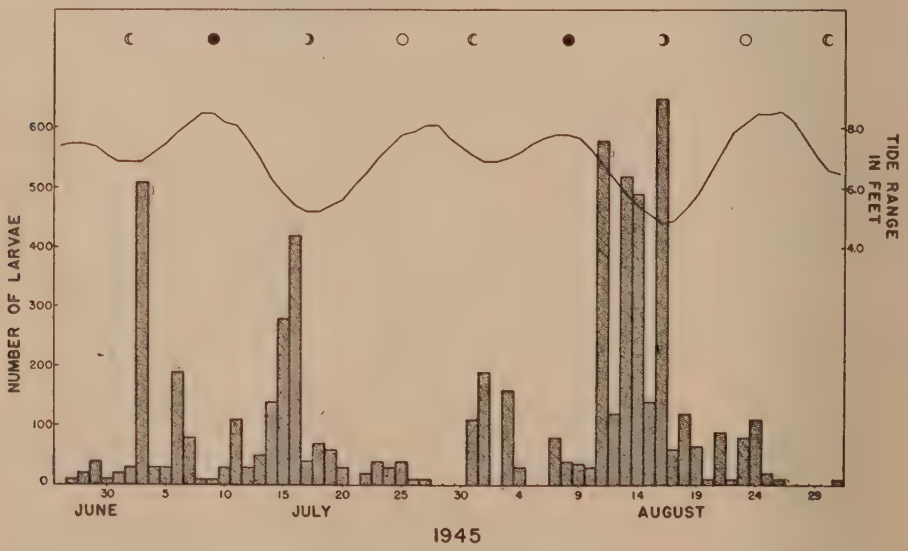

FIG. 4. Numbers of straight hinge oyster larvae per 25 gallons of water collected daily in Milford Harbor during the summer of 1945. Tide range in feet and lunar phases are also shown.

from eggs spawned about 24 to 36 hours prior to collection, are shown.

Perhaps the most important feature common to all three years is that with a few exceptions the larvae were usually least numerous near the new and full moon phases. This observation is directly opposite to that made by Korringa in the Oosterschelde, where he found that "spawning must have had its maxima roundabout the spring tides which occur about 2 days after full and new moon." Our data seem to indicate, on the contrary, that the peaks in the number of straight hinge larvae were usually found near the first or last quarter of the moon (Figs. 2–4). In some instances these peaks either coincided with those phases or occurred one or two days before or after them.

After studying these data one may conclude that in our waters there also are spawning maxima which, however, happen at lunar periods directly opposite to those coinciding with the heavy spawnings of Holland oysters. However, we should hesitate to accept this conclusion because of the following considerations: First, a closer examination of the diagrams would show that although the peaks in the number of straight hinge larvae were often near the first or last quarter of the moon they, nevertheless, did not occur with definite regularity. While many preceded these phases by a day or two, others, such as the peak of July 3, 1945, followed them. In still other instances, as about July 28, 1944, no peak whatsoever was recorded during the first quarter. On the other hand, the peak of September 1, 1944, happened near full moon. Finally, as between August 11 and 16, 1945, large numbers of young larvae were found in the water for several days indicating a continuous and prolonged heavy spawning.

Secondly, the data on the daily number of larvae are available from one station only. In our opinion they are not sufficient for forming a reliable conclusion for the entire oyster-producing section of Long Island Sound. Nevertheless, the data are important in showing that in the area where daily samples were taken there were no definite spawning maxima correlated with the spring tides, occurring about 2 days after new or full moon. On the contrary, the presence of large numbers of young larvae at and near the periods of neap tides suggests that although no well-defined lunar periodicity was observed, the oysters may spawn somewhat more profusely during these phases.

Observations on spawning and setting

In addition to our observations on the daily numbers of larvae we have accumulated other data which may help us decide whether spawning and also setting of oysters in our waters are of a periodical type governed by the lunar phases. These data are based on the observations of the last 13 years, starting in 1937 and including 1949, on the dates of the beginning of spawning and on the dates and intensity of setting in Long Island Sound. We shall start with a discussion of the events prevailing at the beginning of each spawning season.

The beginning of spawning was determined by frequent gross and microscopic studies of oyster gonads and by establishing the date of the first appearance of larvae. Semi-weekly cruises were begun toward the end of June for the collection of samples at all our stations located throughout the most important oyster-producing section confined between New Haven and Bridgeport. The stations were located at approximate depths of 10, 20 or 30 feet. The number of stations established in different years varied from 10 to 19. In addition to the main stations of Long Island Sound several substations were kept in more shallow places, such as Milford Harbor.

When the date of spawning was approaching, many samples, in addition to those taken on the regular trips, were collected daily, or almost daily, from several beds of Long Island Sound and from

Milford Harbor. This method allowed us to determine to a day, or almost to a day, the date of the beginning of spawning.

In our waters the spawning season may be begun by a comparatively few oysters releasing some eggs. Other oysters will follow somewhat later, and in some years ripe but unspawned oysters may be found as late as six weeks after the beginning of the spawning season (Loosanoff and Engle 1942).

Judging by the presence of a few partially spawned oysters, spawning begins about the same time at the majority of stations. The notable exception was the year 1941 when the inshore shallow water oysters began to spawn on July 2, while the oysters living at a depth of about 10 feet and more did not spawn until July 9. We prefer to consider July 2 as the date of the beginning of spawning because the larvae developed from the eggs discharged on that day set later on in considerable numbers, thus commencing the setting season.

Spawning in Long Island Sound begins during the last few days of June or during the first days of July (Fig. 5). The earliest date of spawning recorded was in 1945 and 1949, on June 26, and the latest, in 1937 and 1940, on July 3. Thus, in 13 years the beginning of spawning was confined to the calendar period of only about 8 days.

The beginning of spawning occurred at every phase ranging from new moon to the last quarter (Fig. 5). In 9 out of 13 years it took place near new or full moon. However, it did not occur with any regularity either before or after those phases but with considerable variation in both directions. For example, in 1939, 1940, 1943 and 1947 spawning began 2 or 3 days before new or full moon, in other words, 5 or 6 days before the spring tides, too far away to be regarded as caused or induced by the hydrostatic conditions prevailing at such tides. Considering these circumstances and also that in the four other years spawning began at, or very close to, the first or last quarter

YEAR	MONTH AND DAY	MOON PHASE	TIDE RANGE IN FEET	DEPARTURE FROM MEAN TIDE RANGE
1937	7-3	☾ +2	7.0	+0.4
1938	6-28	● +1	9.6	+3.0
1939	6-29	○ -2	8.1	+1.5
1940	7-3	● 2	7.2	+0.6
1941	7-2	☽	7.1	+0.5
1942	6-29	○ +1	9.6	+3.0
1943	6-29	● -3	7.1	+0.5
1944	6-28	☽	5.2	-1.4
1945	6-26	○ +1	7.4	+0.8
1946	7-1	● +2	8.8	+2.2
1947	7-1	○ -2	6.8	+0.2
1948	6-30	☾ +1	5.3	-1.3
1949	6-26	●	7.4	+0.8
MEAN RANGE OF TIDE 6.6 FEET SPRING RANGE OF TIDE 7.7 FEET				

FIG. 5. Dates of the beginning of spawning during the 13-year period, and moon phases, tide range and departure from mean tide range prevailing at those dates. Signs of plus or minus and numerals indicate that the events shown at the head of the column took place that many days before or after the exact dates of indicated lunar phases.

it may be concluded that the beginning of spawning is not confined to a certain lunar phase.

The beginning of spawning was not related to definite tidal changes and, therefore, changes in hydrostatic pressure (Fig. 5). In Long Island Sound the mean range of the tide is 6.6 feet, and the spring range, being 7.7 feet, is 1.1 feet above the mean range. Were we to assume that spawning begins on the spring tides, about 2 days after full or new moon, and that it is caused by the rhythmical sequence of differences in the water pressure between the neap and spring tides, we would find little support in our data. Only four times in 13 years did spawning begin

during the tide range of 7.7 feet or more (Fig. 5). During the same period departure from the mean tide, at the onset of spawning, ranged from + 3.0 to − 1.4 feet. It is noteworthy that in 1944, a year of good oyster set, the beginning of spawning occurred when departure from the mean tide range was as much as − 1.4 feet.

On the basis of the data discussed above we may form the conclusion that in Long Island Sound the beginning of spawning of oysters should be expected on June 30 ± 4 days, independently of the lunar phases and of the rhythmical changes in hydrostatic pressure resulting from departure from the mean tide range.

Another important event in the propagation of oysters, that may lend itself to the analysis of periodicity, is the metamorphosis of larvae or, as it is commonly called, setting. Because the daily intensity of setting changes sharply during the summer, it is easy to ascertain whether these changes occur with regular periodicity.

The method employed in observations on the beginning, extent and the end of setting of oyster larvae in Long Island Sound has already been described (Loosanoff and Engle 1940). Here it is sufficient to say that with the aid of dissecting microscopes, the oyster set was examined and counted on the surfaces of the oyster shells taken from the collectors brought in twice a week from all our Long Island Sound stations. The collectors were poultry wire-mesh bags filled with clean oyster shells. The shells were always discarded after examination never again to be used in the collectors.

The data on the daily intensity of setting, if used as a proof of the presence or absence of periodicity, should be employed rather cautiously because the intensity depends not only on the number of eggs originally discharged by the oysters on any given day, but also on the rate of survival of the larvae that developed from those eggs. It is possible that a light spawning may give a comparatively heavy set if the mortality of the larvae is low, while a heavy spawning may result in a complete failure if the larvae do not survive. This contention is to some extent corroborated by our field observations (Loosanoff and Engle 1940). Nevertheless, it is thought that within as long a period as 13 years, periodicity, if such exists, should manifest itself regardless of numerous variables which may tend to shade it.

The length of the free-swimming period of the oyster larvae of Long Island Sound has never been accurately determined. Our observations show that the number of days elapsing between the beginning of spawning and the appearance of the first set ranges from 13 to 24, and averages 18.5 days (Fig. 6). The shortest period of 13 days was recorded in 1941, and the longest of 24 days, in 1943. Since, with the exception of 1943, the larval period was never longer than 20 days, it is possible that in 1943, a year when setting of oysters was extremely light, none of the larvae, which hatched from the eggs discharged during the first few days of the season, survived to reach the setting stage.

We found that in Long Island Sound the time and intensity of setting do not follow a rigid pattern from year to year. Nevertheless, in most instances there are at least two distinct waves of setting with definite maxima or peaks. The exceptions were the summers of 1943 and 1949 when second waves were practically nonexistent. The beginning of setting, which usually is also the beginning of the first wave of setting, and the dates of the peaks of the different waves of setting can be quite accurately determined from our records. However, the beginning of the second wave of setting is not always easy to ascertain because in some years setting may continue throughout the summer without having any blank period between the end of the first and the beginning of the second waves. In these cases, which hold true only for 2 or 3 years, the date of the beginning of the second wave was considered to be the day of the beginning

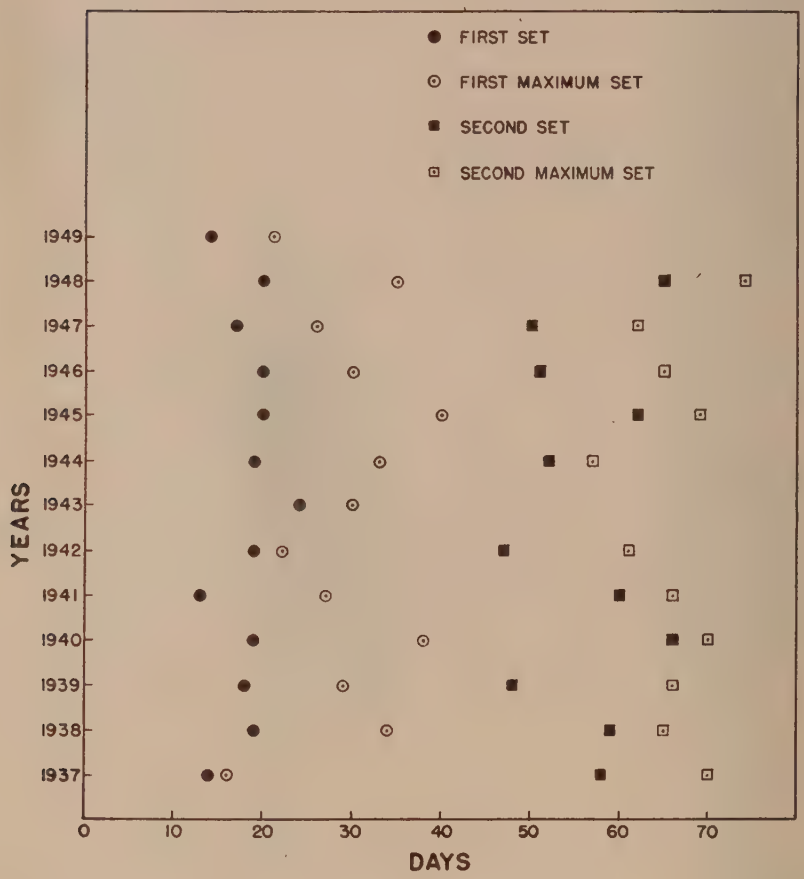

FIG. 6. Days elapsing between the beginning of spawning in each of the twelve years (1937–1949) and dates of first setting, maximum setting of first wave, beginning of second wave of setting, and maximum setting of second wave.

of the trend leading to the second peak of setting.

The following discussion can be better understood by studying Figure 7, which is offered here as an illustration summarizing some of our observations on the daily intensity of setting in Long Island Sound in one of the years of our studies. Similar data and figures are available for the other years. The columns of Figure 7 represent the sum of the daily set in 1948 on the collectors from all our stations located in different areas of the Sound.

The peaks of the waves varied considerably in magnitude in different years and within the same year. In several instances, as in 1948, the two waves of setting were of about the same importance and their peaks were of approximately the same height (Fig. 7). In other years one of the waves decidedly predominated, the other representing only a small percentage of the total annual set. There was no regularity in the relative importance of the two waves because in some years the first wave was the heavier, while in others it was the lighter of the two.

Although in each wave a single day appeared as the peak, the periods of heavy

setting were not confined to those culminating points. Often, as happened in 1948 (Fig. 7), heavy setting, although somewhat varying in intensity, continued quite steadily sometimes as long as 8 to 10 days. This setting may be justifiably regarded as resulting from the continuous heavy spawnings preceding the settings by approximately 18 days, our average figure for the length of the larval period.

In 1948 the beginning of setting was recorded on July 21, about 20 days after the first spawning. The setting showed two well-defined waves (Fig. 7). The beginning of the first was on July 21, and its peak, on August 5, or about 35 days after the beginning of spawning. The second wave, which in 1948 was especially well defined by a long blank period prior to it, began on September 4, 65 days after the beginning of spawning, and its peak, recorded on September 12, was 74 days after the beginning of spawning.

In the 13 years the periods elapsing between the beginnings of spawning and the maximum setting, or the peak of the first wave, varied considerably from year to year ranging from 16 to 40 days and averaging about 30 days (Fig. 6).

The beginning of the second wave of setting varied from 47 to 66 days and averaged 56 days after the beginning of spawning (Fig. 6). In 1943, which was the year of almost complete failure of setting, and in 1949, the second waves were represented only by a few scattered spat at some stations, without showing a definite peak. Because the second waves of 1943 and 1949 were virtually absent, they will not be discussed in this paper.

The maximum daily set of the second wave occurred from 57 to 74 days and averaged 66 days after the beginning of the spawning season (Fig. 6).

Having established the time relation of some of the important events in the propagation of oysters in Long Island Sound we may proceed now to discuss whether these events are confined to certain lunar phases. These events are: the beginning of spawning, beginning of setting, day of maximum setting of the first wave, beginning of second wave of setting, and the day of maximum setting of the second wave.

The conditions at the beginning of spawning have already been discussed and are summarized in Figure 5. It was con-

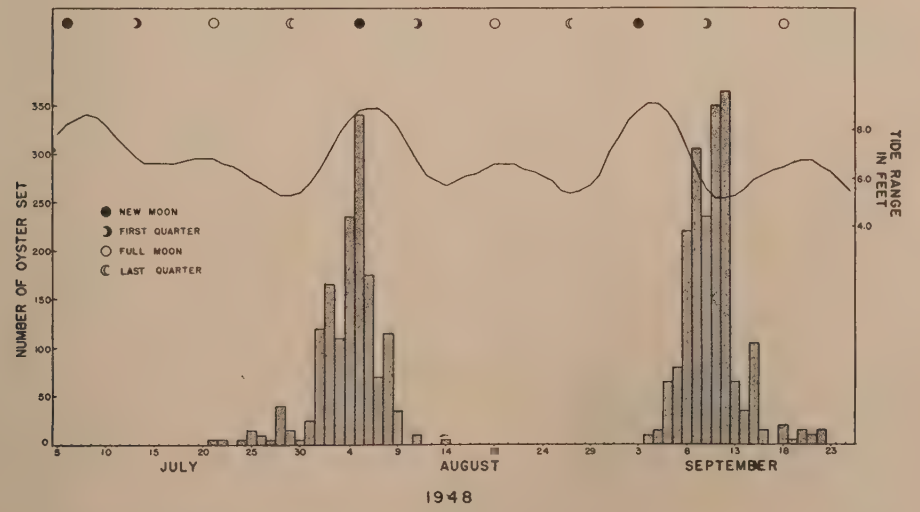

FIG. 7. Daily intensity of setting per 100 shells at ten collecting stations, Long Island Sound, 1948. Lunar phases and daily tide range are also shown.

YEAR	MONTH AND DAY	MOON PHASE	TIDE RANGE IN FEET	DEPARTURE FROM MEAN TIDE RANGE
1937	7-17	☽ +2	5.4	-1.2
1938	7-17	☾ -3	6.7	+0.1
1939	7-17	● +1	9.5	+2.9
1940	7-22	○ +3	7.0	+0.4
1941	7-15	☾ -1	5.8	-0.8
1942	7-18	☽ -3	6.6	0.0
1943	7-23	☾ -1	7.2	+0.6
1944	7-17	● -3	7.5	+0.9
1945	7-16	☽ -1	5.4	-1.2
1946	7-21	☾	6.7	+0.1
1947	7-18	●	9.0	+2.4
1948	7-21	○	6.8	+0.2
1949	7-10	○	7.7	+1.1

FIG. 8. Date of beginning of setting in Long Island Sound in each of the 13 years of observations (1937–1949) and phase of moon, tide range in feet, and departure from mean tide range prevailing at each date.

cluded that the beginning of spawning is not confined to a definite lunar phase.

The earliest beginning of setting was recorded in 1949, on July 10, and the latest, in 1943, on July 23 (Fig. 8). Thus, in 13 summers of observations the beginning of setting was confined to 14 calendar days. However, if, because of the unusual weather conditions prevailing in 1949 we could assume that that summer was an atypical one, then the period could be shortened to only 9 days—July 15–23. Such an assumption is justifiable because of the hiatus existing between the dates of July 10 and 15 (Fig. 8), which indicates that such an early beginning of setting as occurred in 1949 was an unusual phenomenon.

The beginning of setting happened at every moon phase (Figs. 8, 9). In six years it took place at or near full or new moon, while during the seven other summers it occurred either near the first or last quarter. In general, during the 13-year period all four phases were almost evenly represented. Obviously, there was no correlation between the beginning of setting and a definite lunar phase.

The beginning of setting was not confined or even closely related to a certain tide condition (Fig. 8). The tide range on the days of setting varied from 5.4 feet in 1937 and 1945, to 9.5 feet in 1939, and the departure from the mean tide range varied from -1.2 to $+2.9$ feet. In three years setting began when the tide range was less than 6.6 feet, which is our mean range, and only on two occasions, 1939 and 1947, did the beginning of setting happen on the days when the tide range was above 7.7 feet. In three years setting began when the departure from the mean tide range was on the minus side (Fig. 8).

After considering the circumstances under which setting began during the period of our observations we may offer a provisional formula for the prediction of the beginning of setting of oyster larvae in Long Island Sound. The formula is as follows:

The beginning of oyster setting in Long Island Sound should be usually expected on July 19 ± 4 days, regardless of lunar phases and of changes in hydrostatic pressure caused by changes in the tidal level.

This formula is based upon our observations which, we believe, are extensive enough to justify suggesting it. It should be found correct in a majority of instances. Nevertheless, we do not maintain that it is infallible because some extremely abnormal conditions, such as encountered in 1949, may so affect the oysters or their larvae that the beginning of setting may happen outside the limits given in the formula. Furthermore, the possibility always remains that the larvae emerging from the eggs discharged during the first few days of the spawning season may perish and, as a consequence, the beginning of setting may be delayed

until the larvae from later spawnings reach the state of metamorphosis.

The maximum setting of the first wave took place at all moon phases (Fig. 9). In about half the instances it occurred near the first quarter, a circumstance that may be important. This importance becomes even more significant if it is understood that the maximum setting of 1939 and 1944, which in our Figure 9 is shown to occur three days before full moon, can also be interpreted as occurring five and four days after the first quarter. The set of 1946 shown as taking place three days after the new moon can also be shown as happening four days before the first quarter.

Thus, in nine out of thirteen years the day of maximum setting of the first wave occurred near the first quarter. More detailed studies of the data will show, however, that in these nine years maximum setting took place from four days before the date of the first quarter to five days after it, thus extending over a range of 10 days (Fig. 9). Such a period is too long to be included within the short lunar period of one or two days, as Korringa (1947) finds almost always prevailing when a heavy spawning of Holland oysters or a heavy swarming of their larvae takes place. Furthermore, in two other years, 1943 and 1945, the maximum setting was recorded three days before new moon, in other words, 11 or 12 days before the first quarter, and in 1948 it took place on the date of new moon. These observations show that the date of maximum setting of the first wave is not sharply confined to the period of the first quarter or any other lunar phase.

Moreover, as has already been mentioned, heavy setting usually is not completed in a single day, but may continue, with some variations in intensity, for more than a week. For example, in 1948 the period of heavy setting of the first wave extended from August 1 to August 8 (Fig. 7). In relation to the lunar condition it began on the third day after the last quarter and continued 4 days past the new moon date. Obviously, even if in some cases the date of maximum setting coincides or closely approaches a certain

YEAR	MOON PHASES			
	BEGINNING OF SETTING	MAXIMUM SETTING FIRST WAVE	BEGINNING OF SECOND SETTING	MAXIMUM SETTING SECOND WAVE
1937	☽+2	☽+4	☾+2	☽-1
1938	☾-3	☽-2	●+1	☽
1939	●+1	○-3	●+1	☾-3
1940	○+3	☽	☽-1	☽+3
1941	☾-1	☽-2	☽+2	○+1
1942	☽-3	☽	●+3	○+3
1943	☾-1	●-3	—	—
1944	●-3	○-3	●+2	☽-1
1945	☽-1	●-3	☾-3	●-3
1946	☾	●+3	☾+1	☽+1
1947	●	☽+3	☽-3	○+1
1948	○	●	●+1	☽+2
1949	○	☾-1	—	—

FIG. 9. Moon phases prevailing at the dates of beginning of setting, maximum setting of first wave, beginning of second wave of setting, and maximum setting of second wave. Long Island Sound, 1937–1949.

moon phase, the significance of such an event is considerably lessened because the actual period of heavy setting may be so long that during it the changes in the tidal range may go from one extreme to another.

The beginning of the second wave of setting was observed at all phases except full moon (Fig. 9). In five years it occurred near new moon, while during the other six years it was equally divided between the first and last quarter periods. It is clear that in this case there was no relation between it and a definite lunar phase.

The maximum setting of the second wave occurred, as in the first wave, most often near the time of the first quarter. This happened 6 times in 11 years (Fig. 9). It is important, however, that in the other five years it took place at the three other lunar periods, the dates of the setting being removed from the first quarter by 10 days or more. In 1943 and 1949 the second waves of setting were too light to show maxima.

The observations on the second wave seem to minimize somewhat the importance of the first quarter as the period when maximum sets should be expected. Nevertheless, because most of the peaks of both waves happened around the first quarter we may consider this phase, if any lunar periodicity exists, as the period around which our heavy sets are most likely to occur. However, in offering this suggestion it is not implied that the dates of maximum sets in our waters occur with

YEAR	SPAWNING				SETTING		
	ASSUMED DATE OF SPAWNING	MOON PHASE	HIGH HIGH WATER IN FEET	DEPARTURE FROM MEAN TIDE RANGE	MONTH AND DAY	MOON PHASE	DEPARTURE FROM MEAN TIDE RANGE
1937	7-2	☾ +1	7.1	+0.3	7-19	☽ +4	-0.8
1938	7-14	○ +2	6.8	+0.1	8-1	☽ -2	+0.7
1939	7-10	☾ +1	6.5	-0.9	7-28	○ -3	+0.8
1940	7-23	○ +4	6.6	-0.1	8-10	☽	+0.6
1941	7-11	○ +3	7.6	+1.9	7-29	☽ -2	+1.1
1942	7-3	☾ -2	7.2	+1.0	7-21	☽	0.0
1943	7-11	☽ +1	6.6	-0.6	7-29	● -3	+0.1
1944	7-14	☾ +2	7.2	+0.4	8-1	○ -3	+0.4
1945	7-18	☽ +1	6.2	-1.4	8-5	● -3	+0.9
1946	7-13	○ -1	7.0	+0.2	7-31	● +3	+1.4
1947	7-9	☾ -2	6.3	-0.9	7-27	☽ +3	-0.8
1948	7-18	○ -3	7.0	+0.1	8-5	●	+2.2
1949	6-29	● +3	7.4	+0.9	7-17	☾ -1	-1.4

FIG. 10. Moon phases and tidal conditions existing at the dates of spawnings which presumably caused maximum setting of first wave. Long Island Sound, 1937–1949.

YEAR	SPAWNING				SETTING		
	ASSUMED DATE OF SPAWNING	MOON PHASE	HIGH HIGH WATER IN FEET	DEPARTURE FROM MEAN TIDE RANGE	MONTH AND DAY	MOON PHASE	DEPARTURE FROM MEAN TIDE RANGE
1937	8-24	○ +2	7.8	+1.8	9-11	☽ -1	-1.6
1938	8-14	○ +3	7.2	+0.7	9-1	☽	-1.2
1939	8-16	● +1	8.4	+3.2	9-3	☾ -3	+0.3
1940	8-24	☾ -2	6.6	-0.7	9-11	☽ +3	+0.1
1941	8-19	● -3	6.7	-0.4	9-6	○ +1	+1.4
1942	8-11	● -1	7.1	+0.5	8-29	○ +3	+1.2
1943							
1944	8-7	○ +3	8.0	+2.4	8-25	☽ -1	-1.0
1945	8-16	☽	6.1	-1.8	9-3	● -3	+0.3
1946	8-17	☾ -3	7.3	+0.8	9-4	☽ +1	-1.7
1947	8-14	● -2	7.7	+1.5	9-1	○ +1	+0.3
1948	8-25	☾ -2	6.6	-0.7	9-12	☽ +2	-1.4

FIG. 11. Moon phases and tidal conditions existing at the dates of spawnings which presumably caused maximum setting of second wave. Long Island Sound, 1937–1948.

the regularity resembling that of spawning or swarming of European oysters, where the maxima are sharply defined and are confined to one or two days of certain lunar periods (Korringa 1947). On the contrary, in Long Island Sound maximum sets took place in all four lunar periods. Even if many of those occurred near the first quarter, they sometimes happened 3 to 4 days either before or after the exact date of that lunar phase, thus being extended over a long period during which the tidal conditions varied considerably.

Further indication of the absence of periodicity was a lack of uniformity in the departures from the mean tide range during the dates of maximum set of the two waves. These data are given in the right halves of Figures 10 and 11. For the first wave these departures range from -1.4 to $+2.2$ feet, and for the second from -1.7 to $+1.4$ feet. In neither case was there any conclusive evidence that the maximum sets occurred when the departures from the mean tide range were of certain magnitudes. In general, of the 24 maxima of the first and second waves one happened when the departure was 0.0, eight when it was on the minus side, and 15 when it was on the plus side.

TABLE I. *Number of days elapsing between the dates of maximum setting of first and second waves, Long Island Sound, 1937–1948*

Year	Days	Year	Days
1937	53	1943	—
1938	30	1944	23
1939	36	1945	28
1940	31	1946	34
1941	38	1947	35
1942	38	1948	37

Searching further for signs of periodicity in the occurrence of the peaks of the two waves of setting a table was made to show the number of days elapsing between the dates of maximum settings of each year (Table I). The longest period between the two peaks was recorded in 1937, when 53 days elapsed between these two events. The shortest period of 23 days was noted in 1944. In the remaining years the period between the two peaks ranged between 28 and 38 days.

The lunar month is approximately 28 days. Only in 1945 did the number of days elapsing between the peaks of the two waves coincide with this figure. This eliminates the possibility of a monthly periodicity, i.e., a dependence upon a single lunar phase. If a semi-monthly periodicity were involved, as is the case of heavy spawnings of the European oyster (Korringa 1947), then the peaks would be expected to occur at intervals of 14 days. That such periodicity does not exist is shown by our data (Table I).

It is interesting that in six years the period elapsing between the two peaks was from 34 to 38 days, and the average, 36 days. The latter figure would be equal to one lunar month of 28 days plus a period roughly equal to that elapsing from one phase of the moon to the next. Obviously this does not indicate a periodic activity associated with a definite lunar phase and the corresponding tidal condition.

Since the dates of maximum sets are accurately determined, we may try to use this knowledge to ascertain the dates of the spawnings which caused these sets, and subsequently determine during what lunar phases and under what tidal conditions these spawnings took place. We know that the average length of the larval period in our waters, at least during the early part of the season, is about 18.5 days. Therefore, we can go back that number of days from the dates of maximum sets and determine the approximate dates when the spawnings responsible for these sets occurred. Because maximum sets occur in the middle of the summer, when the temperature is usually somewhat higher than at the beginning of the season and, therefore, development of larvae may proceed more quickly, we shall take 18 days, instead of the average of 18.5, for our estimations.

In offering the above-described approach we wish to mention that its accuracy is only relative, because of the differences in the ecological conditions under which larvae have to exist during different years. Nevertheless, it is again believed that periodicity, if such existed, would display itself within a period of 13 years, even if other factors would tend to mask it.

As is shown in the left half of Figure 10, the spawnings that presumably caused the maximum sets of the first waves took place near all four lunar phases. Only once, in 1949, did it take place near new moon, the period when the range of tide in Long Island Sound is greatest. This is in disagreement with observations on the behavior of *O. edulis* of Holland where maximum spawnings usually take place at the height of the spring tides. In five years the spawnings took place near the last quarter, in other words, during neap tides when the range of tide and the differences in hydrostatic pressure were small. This, again, disagrees with observations on the spawning behavior of the oysters of Holland. In two other years, 1943 and 1945, maximum spawning also took place at neap tides one day after the first quarter. In the remaining five years, however, spawning took place near full moon.

It is rather interesting that not once in thirteen years did the date of spawning coincide with the high tide of 7.7 feet or higher (Fig. 10).

Departure from the mean tide range varied at the time of spawnings from -1.4 to $+1.9$ feet, and in five instances spawnings resulting in maximum sets took place during the times when the departure from the mean tide range was on the minus side (Fig. 10).

In analyzing the events of the second wave we will find that the spawnings causing the maximum sets took place at all four lunar phases (Fig. 11). In four years the spawnings took place near the time of new moon, a condition which occurred only once in connection with the first wave. This once more showed the lack of a definite pattern in the relations between the time of the spawnings and the lunar phases.

There was no consistent relation found between the dates of spawnings and the height of high water reached on such dates (Fig. 11). Moreover, the variations in departure from the mean tide range were even greater than recorded for the first wave. These departures varied from − 1.8 to + 3.2 feet. In four years spawnings took place when departure from the mean tide range was on the minus side (Fig. 11).

In summarizing the analysis of the conditions existing during the days when the spawnings presumably responsible for the maximum sets of both waves took place it may be concluded that there is no evidence that these spawnings occurred with a definite regularity which was controlled or influenced by the lunar periods and, therefore, by the corresponding changes in hydrostatic pressure. On seven occasions the spawnings coincided with the spring tide periods (one to three days after new or full moon). On five other occasions they happened at or near the neap tides. In the remaining instances they took place at different intermediate points lying between the two extremes. In nine cases out of 24 the spawnings took place when the departure from the mean tide range was on the minus side, and only in three cases did they happen when the high water level was greater than 7.7 feet—the average of our spring range of tide (Figs. 10, 11).

It may be suggested, as a criticism of our approach, that the 18-day period, which we took as the average required for the larvae to reach metamorphosis, is too long because, as the summer progresses, the water temperature becomes warmer and the length of the larval period decreases. Such a criticism may be justifiable. However, even if the larval period were shortened to 17, 16, 15 or even 14 days, the assumed dates of the spawning would still coincide in most years with periods other than those of the spring tides. Thus, regardless of the changes in the length of the larval period the results still would suggest that the heavy spawnings took place at widely different lunar phases and correspondingly different tidal conditions.

Discussion

Observations carried on in Long Island Sound during the 13-year period, 1937–1949, showed no definite relationship existing between the major events in the propagation of oysters and the lunar phases. In general, all the important events, such as the beginning of spawning, beginning of setting, dates of heavy spawnings and dates of maximum sets, happened at all four lunar phases and, therefore, under widely different hydrostatic conditions caused by the tidal changes.

The data so far available seem to indicate that spawning of *O. virginica* of our waters is not of the periodic nature, such as that found by Korringa (1947) for *O. edulis* of Holland where "maxima of greater and lesser importance in the extrusion of the eggs occur at spring tides (2 days after full and new moon)." However, in comparing some aspects of the propagation of *O. virginica* with those of *O. edulis* we should again emphasize that we are dealing with two widely different types of oysters, and also with two different complexes of ecological conditions. It is only natural, therefore, that our conclusions should differ from those of Korringa.

Korringa thinks that the rhythmical sequences of the differences in water pressure from the neap to the spring tides, and conversely, exert their influence on the oysters of the Oosterschelde during

their breeding period. If comparable differences were not also a regular event in our waters, we could assume that the differences in the spawning behavior of our oysters and those of the Oosterschelde were due to that cause. However, since our vertical tidal movements are also of considerable magnitude, such an explanation is unsatisfactory. In our waters the mean range of tide is 6.6 feet and the spring range is 7.7 feet. On some days, for example, on July 18, 1943, the height of our high water was + 8.7 feet and the low water was − 0.7 feet, thus, the difference between the two tidal levels on that day was 9.4 feet, or over 3 meters. The difference between the high and low water levels for that day at Zierikzee, located at the entrance to the Oosterschelde was, according to Tide Tables of the Atlantic Ocean published by the U. S. Coast and Geodetic Survey, 11.4 feet, or only 2 feet greater than at our station. It is rather doubtful that such a comparatively small difference in tidal range could be responsible for the striking differences in the behavior of the oysters at the two places.

The geographical distribution of *O. virginica* and the range of the tidal conditions under which it exists in nature make it improbable that its spawning is controlled by certain rhythmical changes in the hydrostatic pressure taking place between the neap and spring periods. In general, the natural population of oysters and the extent of the natural oyster beds on our Atlantic coast increase proceeding South. On the other hand, the tidal range decreases from North to South, and in the Gulf of Mexico, where extensive oyster beds exist, the difference between the high and low water levels is often less than 1 foot. Yet, regardless of such small differences between the tidal levels and obviously insignificant rhythmical changes in the hydrostatic pressure, the oysters living in those areas propagate normally.

It is also interesting that, as every experienced investigator has noticed, oysters kept under laboratory conditions in the summer time spawn profusely regardless of the condition of the moon or the stages of the tide in the open water. For example, in our laboratory some spawning oysters may be noticed almost every day during the summer. These oysters, which are kept in shallow trays, are covered with only two to three inches of running water supplied from the storage tank, which is always automatically filled by pumping one hour before high tide. Because the water level over the oysters remains the same, the difference in the hydrostatic pressure cannot be considered as the factor inducing spawning.

It is possible, of course, that, as we have already said, some differences in the spawning behavior of the two species may exist because one of them, *O. virginica,* is oviparous, while the other, *O. edulis,* is larviparous. Furthermore, while the first remains usually of the same sex during the entire spawning period, the second may change its sex several times during the summer. Thus, a comparison of the spawning habits of these two species may be difficult. Because of this consideration one would prefer to compare the behavior of two larviparous species to see whether both are influenced in the same way by the periodic tidal differences associated with certain lunar phases. Such a comparison is possible between *O. edulis* and *O. lurida,* as based on the observations of Hopkins (1937) and Korringa (1947).

As has already been mentioned, Hopkins reported no lunar periodicity in the spawning of *O. lurida.* Its spawning was a continuous process extending for a period of 5 to 6 months. In reference to its intensity Hopkins says "after it once begins, the frequency of spawning slowly increases to a maximum, then gradually diminishes until gravid individuals are found only occasionally." Critical examination of Figure 15 of Hopkins' paper, giving the range of tide and the numbers of "white" larvae (young larvae, just recently developed from eggs) found in 1932, shows that during that season there was only one instance, on May 23, when

a large number of larvae occurred during the spring tides. At other periods of the spring tides, about June 8 and 19, and July 7 and 19, young larvae were conspicuously absent. On the other hand, considerable numbers of larvae were often found in samples taken during the neap tide periods. In general, throughout the season, the larvae were more numerous during those periods than during the spring tides. It is apparent, therefore, that Hopkins found no periodic outbursts of spawning confined to the spring tides which follow new and full moon.

It is significant that Hopkins said: "It has frequently been noted that spawning is most likely to begin during or shortly after a period of neap tides." Although this statement does not refer to the maxima in spawning it shows, nevertheless, that such an important event as the beginning of spawning of the oyster population often takes place during lunar periods, which are opposite to those considered necessary to induce profuse spawning in the oysters of Holland. Naturally, it is difficult to conceive that if definite changes in hydrostatic pressure, which are correlated with the lunar phases, are necessary to induce heavy spawnings, an entirely different set of tidal conditions would be needed to cause the first spawning of the season.

We cannot explain the difference in the spawning behavior of *O. lurida* from that of *O. edulis* on the ground that the tidal differences in Puget Sound are considerably smaller than those in the Oosterschelde. On the contrary, they are of greater magnitude. According to Korringa (1947) in the Oosterschelde the tidal range of the spring tides is about 3.9 meters, and of the neap tides, 3.0 meters, the difference being only about 0.9 meters, or less than 3 feet. In the area of Puget Sound, where Hopkins conducted his studies, the range of the spring tides is about 19 feet (6.3 meters) and that of the neap tides, about 10 to 12 feet (3.3 to 4.0 meters). Thus, in Puget Sound the difference between the spring and neap tidal ranges is about 6 feet, approximately twice as much as in the Oosterschelde. Yet, regardless of almost twice as great a range of tide in Puget Sound and of much more pronounced differences in hydrostatic pressure, *O. lurida,* the species so closely related to *O. edulis,* showed no evidence of heavy spawnings at the spring tides, as Korringa reported for the oysters of the Oosterschelde. On the contrary, some of Hopkins' (1937) data suggest that profuse spawning often occurred at the neap tides.

Louis Lambert, General Inspector of the Office of Scientific and Technical Marine Fisheries of France, who recently visited the United States and with whom we discussed periodicity of spawning of *O. edulis* and swarming of its larvae, thinks that so far no such periodicity has been established or observed in the breeding of *O. edulis* along the coast of France. Korringa (1947) in discussing the work of French oyster biologists also found no support for his theory in their work. He believes, however, that the data offered by some of these investigators are not sufficient to decide whether there is a periodicity in the breeding of French oysters.

Thus, so far, periodic heavy spawning of oysters associated with new and full moon, and consequently, with spring tides, has been found only by Korringa for *O. edulis* of the Oosterschelde, Holland. Neither does *O. edulis* of other geographical regions nor the closely related *O. lurida* of Puget Sound show such periodicity. Since Korringa's conclusions are based upon a definite method of collecting field data, it may be desirable to evaluate the merits of his methods.

Korringa's samples were collected from one station at Yersche Bank, which is located in the center of the Oosterschelde basin (Korringa 1947). The larvae were collected by pumping and filtering 100 liters of water through a plankton net. During the most important part of the reproductive season the samples were taken daily, while during the beginning and the latter part of the season they

were collected every second day. The collection of samples was usually made at low water slack.

Yersche Bank is located in the southeastern half of the Oosterschelde, which is approximately 17 kilometers long and 10 kilometers wide (Korringa 1941). The Bank itself is at least 7 or 8 kilometers long and approximately 3.5 kilometers wide. The question that naturally arises is how well a single sample taken from such a large area represents the conditions existing there.

The experience of one of us in Long Island Sound and Chesapeake Bay with larvae of *O. virginica,* and in Puget Sound with *O. lurida* would make us hesitate to form a conclusion on the distribution and on the numbers of larvae present in any large body of water on examination of a single sample. Our observations, as those of other American investigators, have shown that larvae, as a rule, are not uniformly distributed even over small areas. While a plankton sample collected at one point may contain a large number of larvae, another sample, taken simultaneously, or a few minutes earlier or later, at another point, only a few feet away from the first one, or at the same point but at a somewhat different depth, may contain none or very few larvae. For example, Nelson and Perkins (1931), studying the vertical distribution of larvae of *O. virginica* in Barnegat Bay, New Jersey, found that the number of larvae varied within one meter's depth from 140 to 35,750 per 50-liter sample. It is obvious, therefore, that no reliable conclusions, as to the numbers of larvae in a large body of water, can be formed on the basis of examination of one or two samples.

Korringa (1941) realized the imperfection of his method because in his discussion of horizontal distribution of larvae in the Oosterschelde in general, and also in the center of Yersche Bank, near which his collection station was located, he stated: "The amplitude of the number of larvae during swarming in the centre itself is a less reliable measure, as it is affected by the degree of proximity of the liberating adults. Thus, the enormous number of larvae (2000 per 50 litres) in a sample collected on the 14th of July 1937 at the station Yersche Bank, for instance, did not point to a heavy swarming, for the diagram (Fig. 8) clearly shows that it must be attributed to the immediate proximity of one (or more) liberating adult(s)." In his article Korringa did not explain when unexpected swarmings should or should not be ascribed to the proximity of liberating adults. Neither did he offer any proof that many maximum swarmings, on which he based his theory of lunar periodicity, cannot be attributed to exactly that cause. However, in a recent personal communication to us he clarifies this point considerably by saying: "Indeed, an objection against my sampling station is that sudden occurrence of young larvae just expelled from mother oyster may cast doubt on the value of a sample. That occurred on the 14th of July and once again in a more recent year. To avoid this difficulty, I always compare 2 samples of the same station, one taken at high tide, one at low tide. Only if those yield approximately the same number of larvae, I dare to adopt the figure for use in spatfall prediction. As a rule the two figures come quite close to each other, though entirely different water masses are encountered in two samples."

In offering a criticism on the inadequate data given by Korringa to support his theory we refer only to the material presented in his 1947 article, which is based on a series of observations made at only one station. There is no doubt that Korringa may be able to offer additional data, based on observations at several other stations situated at various points of Yersche Bank, which will further strengthen his extremely interesting theory.

In conclusion, it should be remembered that the factors inducing spawning of oysters are numerous and their interrelations are extremely complex and, at

present, not well understood. Further studies of the physiological conditions of oysters during the pre-spawning and spawning seasons and studies of the influence of the ecological factors on maturation of the gametes should eventually provide the explanation for certain peculiarities in the spawning behavior of different species and genera of oysters.

Summary

1. Observations made during the 13-year period, 1937–1949, showed that spawning of oysters in Long Island Sound began during the last few days of June or during the first days of July. The earliest date of spawning recorded was on June 26, occurring in 1945 and 1949, and the latest, on July 3, in 1937 and 1940.

2. The beginning of the spawning season occurred at all four lunar phases and at widely different tidal conditions.

3. It may be formulated that in Long Island Sound the beginning of spawning of oysters should be expected on June 30 ± 4 days, independently of the lunar phases and of the changes in hydrostatic pressure resulting from the departures from the mean tide range.

4. Daily counts of straight hinge oyster larvae during three seasons showed that there were no definite spawning maxima occurring exclusively within the spring tide periods. On the contrary, the larvae were more numerous during the neap tides.

5. The beginning of oyster setting happened at every moon phase and was not confined or related to definite tidal conditions.

6. It may be provisionally formulated that the beginning of oyster setting in Long Island Sound should usually be expected on July 19 ± 4 days, independently of the lunar phases and of the changes in hydrostatic pressure caused by changes in the tidal levels.

7. In Long Island Sound the time and intensity of setting do not follow a rigid pattern from year to year but, nevertheless, in most instances there are at least two distinct waves of setting with definite maxima or peaks.

8. The peaks of setting vary considerably in magnitude in different years and within the same year.

9. The number of days elapsing between the beginning of spawning and appearance of the first set ranged from 13 to 24 and averaged 18.5 days.

10. The period elapsing between the beginning of spawning and maximum set or peak of the first wave varied from year to year ranging from 16 to 40 days and averaging about 30 days.

11. The beginning of the second wave of setting varied from 47 to 66 days and averaged 56 days after the beginning of spawning.

12. The maximum daily set of the second wave occurred from 57 to 74 days after the beginning of spawning.

13. In general, it was found that in Long Island Sound no definite relationship exists between the important events in the propagation of oysters and the lunar phases. All the events, such as beginning of spawning, beginning of setting and dates of maximum sets, may happen at any of the four lunar phases and, therefore, under widely different hydrostatic conditions.

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ERRATUM

In the paper by Nash, "Associations between fish species in tributaries and shore waters of western Lake Erie," published in Ecology, Vol. 31, the formula for *phi* (p. 563) should include a square root sign over the denominator.

NOTES AND COMMENT

THE VEGETATION OF A BURN NEAR BLANEY LAKE, BRITISH COLUMBIA

Introduction

In 1945 a project was started to investigate the factors controlling regeneration in an area of the forest of the British Columbia coast range. It was conducted under a grant of the British Columbia Industrial and Scientific Research Council and directed by the Department of Biology and Botany and the Department of Forestry of the University of British Columbia. The writer was concerned, in 1948, with the study of a number of permanent sample plots to the south and west of Blaney Lake in the University Forest. Some of the plots were located in a second growth stand and others in a logged and burned area to the westward. A study of the vegetation, soil and microclimatic conditions of the plots was made to discover the possible causes of the stages in succession then present and their probable course of development.

The University of British Columbia Forest lies about 35 miles from the Pacific Coast, east of Vancouver and about 5 miles north of Haney on the Fraser River. It is on the south end of the coast range batholith, the bedrock being granite or quartz diorite, in places overlain by glacial till. The soils are mostly gravelly and sandy, podsolic and acid. The topography is fairly steep and much dissected by stream courses. The altitude of the area examined varies from 1,000 feet to 1,200 feet above sea level.

For the years 1946 to 1948 the average annual precipitation has been 95 inches. The Forest is within the area described by Thornthwaite (1931) as microthermal, wet, rainfall adequate at all seasons; normally, however, there is little rainfall during July and August. The climax forest type can be referred to the cedar-hemlock association of the Coast Forest Formation described by Weaver and Clements (1938). *Thuja plicata* (western red cedar), *Tsuga heterophylla* (western hemlock), and *Pseudotsuga taxifolia* (Douglas fir) are common and *Abies amabilis* (Pacific silver fir) is occasionally present.

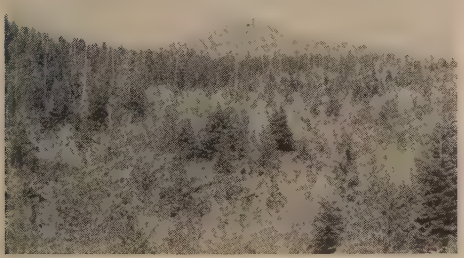

Fig. 1. The burn, looking north up the valley, showing the poor coniferous regeneration after 20 years. Several dense groups of conifers are evident.

The whole area suffered a severe burn about 90 years ago, and most of the standing timber is second growth from 45 to 85 years old, although there are some areas of mature trees. From 1925 to 1928 an area of several square miles was clear cut. Part of this area within the Forest was slash—burned in 1925 and the rest in 1926. Several blocks of seed trees were left, but these soon blew down. The area burned again in 1931, and most of the regeneration that had become established was killed.

The plots are situated in the valley bottom and on either side of a valley which runs from north to south. The logged and burned area extends to the western side of the valley bottom (fig. 1).

Vegetation of the Burn

Spilsbury and Smith (1947) proposed some forest site types for Douglas fir stands of the Pacific Northwest, but little has been done on the vegetation types of burns for the British Columbia coast forest. This paper gives a description and classification of the vegetation encountered. These "types" are of course transitory and often confined to small areas, largely controlled by local variations in topography, soil, and availability of seed. The plots cover a relatively small area of the forest and burn, and since early successional stages are so subject to local variations the conclusions are valid for this restricted area only. Table I presents

Table I. *Average soil conditions for vegetation types (at depths of 1–3″)*

Vegetation type	pH	Water content, per cent	Organic matter content, per cent
Tangle	5.1	115	40
High bracken	5.2	50	18
Medium bracken	4.5	35	14
Low bracken	5.0	25	10
Dense coniferous regeneration	5.0	50	18
Conifers in dense groups	4.9	30	16
Vine maple groups	6.0	40	15

the pH, water content (air dried), and organic matter characteristic of the soils of the various types of vegetation.

Rock types

Bare rock, rock covered by lichens, and rock covered by mosses were grouped as one type, for although they represent three distinct stages in succession they are essentially without soil and unfavorable for growth of vascular plants without considerable modification. *Polytrichum juniperinum* and *Rhacomitrium canescens* were the most common mosses found and they formed extensive mats where there were slight depressions in the rock. Their rhizoids were in a half-inch layer of organic matter and decayed rock.

Swamp types

Swamps developed both where streams spread out and in ill-drained depressions where there was standing water all the year. Water flow was quite noticeable in the stream areas, particularly after heavy rain when its speed increased considerably and the level often rose 6 inches or more. Many of the swamp areas were open, but dense willow thickets had developed in others. Temperatures were generally lower than in the surrounding areas, but relative humidities were often lower than might have been expected (lowest recorded 38%) because wind blew up the stream courses.

Open swamp.—The characteristic vegetation consisted of herbs (which grew rooted in the mud in about 9 inches of water), although scattered willows were present. Common herbs were *Lysichiton americanum* (skunk cabbage), *Athyrium filix-femina* (lady-fern), *Oenanthe sarmentosa* (water parsley), *Habenaria saccata* (rein orchid), *Carex* spp. and *Sphagnum* sp. Where logs were present, *Thuja plicata, Gaultheria shallon* (salal), *Menziesia ferruginea*

Fig. 2. A salmonberry tangle in a damp depression (5 Sept. 1948). In the background there was a willow thicket lower in the depression.

Fig. 3. A salmonberry tangle around a temporary stream bed within the second growth timber, showing the absence of trees in the tangle area (8 Aug. 1948).

(false azalea), and *Vaccinium ovalifolium* (tall blue bilberry) made more or less stunted growth on them. Cladonias and mosses were also common.

Willow thickets.—*Salix* spp. 20 or more years old and up to 18 feet high stood in dense thickets where the surface water was about 9 inches deep. *Oplopanax horridum* (devil's club) was sometimes present, and Carex and Sphagnum were common around the bases of the willows at water level (fig. 2).

Tangle types

In depressions where the soil was damp, but where there was no standing water, at least in summer, shrubby species formed dense tangles (figs. 2, 3). The most common species was *Rubus spectabilis* (salmonberry), with *R. parviflorus* (thimbleberry) and *Spiraea douglasii* (hardhack) less common. The *Rubus spectabilis* was from 2 to 6 feet high, varying chiefly according to soil moisture. Other common species which completed the denseness of the tangles to ground level were *Gaultheria shallon, Rubus macropetalus* (blackberry), *Athyrium filix-femina,* and *Epilobium angustifolium* (fireweed). Such tangles occupied a considerable area of the burn.

Bracken types

Since few areas were occupied exclusively by *Pteridium aquilinum* (bracken), the bracken types are defined as those areas where bracken occupied more space than did conifers. According to which tree species had the greatest frequency, the bracken types were divided into bracken with hemlock, with cedar, or with Douglas fir or a combination of these species. The bracken itself could be divided into three height classes which reflected the quality (water content and fertility of the soil) of the site at that time.

High bracken.—The bracken grew to a height of 5 feet or more. It was dense, often allowing little light to reach the ground (10% of full daylight). Common species growing with the bracken were *Epilobium angustifolium, Cornus canadensis* (bunchberry), *Rubus macropetalus,* and *R. spectabilis.* Where the bracken was very dense, the other species were reduced to an understorey and their flowering was sparse. High bracken developed where there was favorable soil moisture and high organic content.

As in all bracken types, aspection was marked. In winter, snow pressed down the old fronds so that by spring a continuous carpet of litter up to 5 inches thick was present, with few other plants visible (fig. 4). The bracken reached its maximum growth by the middle of June and began to fall again by early September. Temperatures under the bracken were much lower than above when it was fully grown, but in early summer temperatures of up to 100° F were recorded on the surface of the litter.

Medium bracken.—This was the most common bracken type, the Pteridium being about 4 feet high, dense, but not dense enough to prevent the accompanying species listed above from reaching full development. *Anaphalis margaritaceae* (pearly everlasting), *Gaultheria shallon,* and *Lycopodium clavatum* were also common. While coniferous seedlings were less infrequent than in the high bracken type, they were still not dominant. Soil surface temperatures were somewhat lowered due to the shade of the bracken, but still reached 100° F. Relative humidities as low as 35 per cent were recorded.

Low bracken.—On excessively drained, burned, and eroded areas the bracken grew to only about 2 feet high. The litter was thin and patches of mineral soil were exposed. Common plants, also low growing, included those of the medium bracken type and in addition *Spiranthes romanzoffiana* (ladies' tresses), *Solidago lepida* (golden rod), *Hieracium albiflorum* (hawkweed), and *Hypochaeris radicata* (cat's ear). Grasses also occurred sparsely but in this region they are of little importance in succession, their rôle being filled by Pteridium and other ferns. This type was subject to excessive soil temperature, 90° F being recorded at a depth of 3 inches.

Fig. 4. The bracken debris in early summer (end of May 1948) at the beginning of the new year's growth. To the left and right rock types can be seen.

Fig. 5. Dense coniferous regeneration, here mostly *Thuja plicata* in the strip close to the forest. The conifers have invaded medium bracken (6 Sept. 1948).

Coniferous tree types

The pattern of coniferous regeneration was largely controlled by the effective distance from the seed source. As the prevailing wind blows up the valley from the south, parallel to the edge of the green timber, effective distance of reseeding was only about 300 feet.

Dense coniferous regeneration.—In the valley adjacent to the green timber, which acted as a continuous seed source, dense coniferous regeneration had occurred (figs. 5, 1). *Tsuga heterophylla* was the most common species, though in some areas *Thuja plicata* was more frequent, and Pseudotsuga formed only about 5 per cent of the tree cover. Bracken, mostly of the medium type, occupied the areas between the trees. Where the trees were particularly dense the bracken merely weaved in between the branches. Species characteristic of the medium bracken type were also found. Although older trees were found, most of the dense regeneration examined was not much more than 10 years old; that is, the seeds had apparently germinated 7 or 8 years after the last fire.

The influence of direction of slope on the density of regeneration was noticeable. On some north slopes only a few feet high, trees were much denser and had grown faster. There was also greater germination of seeds or higher survival of seedlings or both on the shaded sides of logs and other debris, and in some cases dense groups of small Tsuga seedlings were found in these places.

Conifers in dense groups.—Tsuga and Thuja,

with the former usually more numerous and the latter sometimes absent, formed dense groups covering from a few to 20 or more square feet. The trees were usually about 18 years old and had made good growth, being up to 20 feet high. In the center of the group a "chamber" was formed by the death of the lower branches of the central trees. The light intensity in this chamber was very low (2% of full daylight) because the outer branches extended almost to the ground. Herbaceous flora within the chamber was sparse and consisted of tolerant forest floor species such as *Polystichum munitum* (sword fern), *Struthiopteris spicant* (deer fern), *Trillium ovatum, Tiarella* sp. and *Linnaea borealis* (twin flower). A thin layer of needles covered the ground. Such isolated groups were found on average sites, but on the north slopes of several gullies similar trees formed continuous cover.

Deciduous trees

On these uplands deciduous trees are not important constituents of seral stages. *Alnus rubra* (red alder), so characteristic of logged valley bottoms, was found only in an old railway cutting. Scattered trees of *Prunus emarginata* (cherry), *Betula papyrifera* var. *commutata* (western paper birch), and *Populus trichocarpa* (black cottonwood) were present but were of little cover value except where the last two had invaded the old railway grade. *Acer circinatum* (vine maple) and *Salix* spp. (in the swamp areas) were the only deciduous trees to assume local importance.

Vine maple groups.—Acer circinatum was common throughout the burn. It varied from a few branches in a clump to extensive groups (40 square feet or more) of 25-year-old stems, forming a characteristic grove. An extensive litter of maple leaves was present. *Cornus canadensis,* Tiarella, Trillium and other tolerant species were common. Some of the older groups were about 20 feet high and were moderately open below the canopy. The younger ones were lower and formed a central chamber with low light intensity.

Discussion

It was observed that, after logging and burning in this area, secondary succession took varied courses and progressed at different rates. Some of the factors which appear to be influential in effecting this variety are the vegetation prior to logging, edaphic conditions, availability of seeds, and microclimatic conditions.

In the forest, before logging, there are relicts of several types of vegetation which reach their best development on the burn. Swampy areas of *Lysichiton americanum* occur. The willow thickets associated with streams and wet places may largely escape burning and can invade adjacent areas of cleared ground. In damp depressions and openings, straggling etiolated salmonberry tangles are found. When the forest cover is removed these plants increase rapidly in density and start fruiting, acting as a seed source for the surrounding area. Bracken occurs throughout the green timber as frail fronds, relicts of a former open stage. It spreads rapidly by means of the rhizomes after logging and burning. Vine maple groups are also relatively common within the forest. Those branches that escape burning provide seed shortly after a slash burn and sprouting from the basal crowns may replace the burned stems. In clear cutting most of the suppressed conifers are destroyed and do not survive to act as a seed source.

The edaphic conditions of the bare rock and the swamp types represent extremes that are not immediately available for reoccupation by conifers, while the rest of the land probably remains more or less suitable. Particularly where the soil within the forest was thin, fire and erosion following the removal of the plant cover have exposed bare rock. Much of the area is sloping, so that erosion has been an important factor in the reduction of the depth and fertility of the soil, a process started by the burning off of the forest litter. Water content of the soil depends largely on topography. In the more level parts of the burn there are small depressions which have favored the accumulation of damp soil. In many cases tangles have developed in these, forming thick layers (up to 8 inches) of raw peat. Intermediate between the rock and swamp types are soils of varying thickness and water content, on which the various types of bracken and conifers are found. On the exposed parts of the eastern ridge Tsuga was less common than elsewhere and Douglas fir, though by no means abundant (35 per acre) was the most frequent tree. This is probably due in part to the better tolerance of the Douglas fir to arid conditions, but at least partly to a better Douglas fir seed source in this area.

The disseminules responsible for the establishment of the tangles are spread rapidly and widely. Many are succulent (e.g., Rubus) and are spread by birds, while others are light and fluffy (e.g., Epilobium) and wind dispersed. Added to this is the fact that many of the species quickly regenerate from forest relicts and act as seed sources. *Acer circinatum* seeds are also rather widely dispersed. Although blocks of seed trees were left on the burn, apparently they blew down before the accidental fire in 1931 and therefore established little regeneration. Some of the dense groups may be attributed to them. Some individual trees and groups established before or shortly after the 1931 burn were beginning to form cones at the

time of the present investigation. These groups would help to speed up regeneration. In this area dense coniferous regeneration in the valley bottom was confined to a narrow belt only a few hundred feet wide along the edge of the green timber; this has resulted from the fact that the prevailing southerly wind is parallel to the margin of the seed source. The dense regeneration mostly of Tsuga and Thuja reflected the species composition of the adjacent forest. On the exposed east-facing ridge, Pseudotsuga was more common than elsewhere. Here also were the largest stumps of this species. This observation suggests that Douglas fir does best on hot exposed areas, but there may be another explanation since an area of Douglas fir forest occurs about a mile to the south and supplies seed from that direction.

Temperatures well over 100° F were recorded on the surface of the bare unshaded mineral soil here. Considerably more Tsuga seedlings were found in shaded areas than in exposed places, so that temperature and moisture may be important factors limiting growth of these seedlings. Low humidity and low soil moisture coupled with high temperatures of the months of low rainfall may be sufficient to kill seedlings, but probably equally important is the fire hazard. The litter of the brush, particularly of the bracken, is highly inflammable. Fire during the early stages of development of these conifers is disastrous, as is only too well demonstrated by the poor regeneration of this burn. The low light intensity under deciduous trees which develop on some burns in the coast range is also believed to be a factor preventing regeneration of Douglas fir. However, in this area deciduous trees were infrequent so the light factor is probably of minor importance compared with competition for ground and availability of seed.

Finally, the vegetation as it was at the time of the investigation may be considered in relation to its probable effect on the course and speed of succession.

The rock areas are normally invaded by bracken and grasses. These make stunted growth for some time, but on account of the severity of the edaphic conditions return to the forest climax is very slow. It is probable that the surrounding area will develop tree cover, shading the rock and mosses, before succession on it has gone far. In the forest, carpets of *Hylocomium splendens* were characteristic ground cover over rock. If left undisturbed this moss carpet would probably be invaded by trees eventually, but under conditions of logging or natural fires, a moss carpet is likely to remain more or less indefinitely.

The wet substratum of the swamps is unsuitable for coniferous invasion. The open swamp may be invaded by willows, and the edge may become more solid and occupied by a salmonberry tangle. The wet depressions remain swampy after the surrounding area has returned to forest and are likely to remain so when the surrounding area is periodically deforested.

When tangles occupy a considerable area and are very dense, conditions for invasion by conifers are unfavorable. The salmonberry tangles found in damp places under a gap in the forest canopy (fig. 3) represent the failure of conifers to occupy the area, rather than the development of the tangle within the forest.

As can be seen from the dense regeneration belt near the green timber, conifers will eventually replace bracken when the seed source is sufficient and continuous. In local areas where litter is very thick, the seedbed is unsuitable and regeneration may be slowed down. Bracken, when it does not offer too much competition, may even be beneficial in providing shade to reduce excessive temperatures. The dense coniferous regeneration is likely to develop into a dense even-aged stand. In the forest, groups of trees occurred which represented those conifers in dense groups found on the burn. Locally, vine maple groups, due to their shade, will resist coniferous invasion and persist in the forest, but the area covered by this species is not great and its effect is of minor importance.

In conclusion it can be stated that logging and burning help to maintain the swamp and rock types, which are unsuitable for forest growth, and that the tangle and tall bracken types attain sufficient density to retard regeneration of the forest. Other types, where soil conditions are more suitable, do not quickly return to forest when they are beyond the short effective seeding distance of the forest trees.

Summary

1. An investigation was made of a logged and burned area and adjacent second growth stand near Blaney Lake, in the University of British Columbia Forest. The object was to trace the succession after logging and to suggest factors influencing its course and rate in this area of the coast forest.

2. The following vegetation types were recognized on the burn: a. Rock types; bare rock, rock covered by lichens, and rock covered by mosses. b. Swamp types, where there was standing water. Open swamps were characterized by *Lysichiton americanum* and other parts were occupied by willow thickets. c. Tangle types, of shrubs (chiefly *Rubus spectabilis*) which develop densely in depressions. d. Bracken types, which were subdivided according to the most common tree species occurring with the bracken. The height and density of the bracken reflected the present quality of the site. e. Coniferous types, which depended largely on the availability of seed. Where a seed source was

sufficiently close, dense even-aged regeneration took place. In other areas fortuitous circumstances gave dense, often isolated, groups of trees. f. Deciduous trees, at the altitude investigated, were scattered and of little cover value, except for local areas of vine maple.

3. Some of the factors considered influential in the course and rate of succession were: a. The relicts of vegetation found in the forest, which reached their best development on the burn. b. Edaphic conditions, which ranged from bare rock to swamps, were responsible for the development of tangles or bracken and conifers. c. Distribution of conifers was largely controlled by the short effective distance of seeding, so that most of the burn was understocked. d. High temperatures and low humidities may have had some influence on conifer distribution but were equally important as a source of fire hazard.

4. Some of the effects of the present burn vegetation on the rate and course of succession were: a. The rock types were unlikely to return to conifers for a very long time and would probably remain within the forest. b. The swamp and tangle types, where well developed, would also retard return of the forest and would be likely to persist after its development. c. Bracken types can be invaded, provided there is sufficient conifer seed; but bracken remains within the forest. d. Dense coniferous regeneration will develop into dense even-aged stands. The conifers in dense groups act as a local source of seed on the burn and are found in the forest. e. The vine maple groups may resist coniferous invasion and persist in the forest, but are of only local importance.

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A BROMELIAD HERPETOFAUNA IN FLORIDA

Bromelias, commonly called "air-plants" or "wild pines," are characteristic plants of the tropical and subtropical regions of America. The majority of species are epiphytes whose leaves catch and hold water in the axils. In the tropics, many species of vertebrate and invertebrate animals inhabit bromelias, especially during dry seasons, when the only water readily available above ground may be provided by these plants (Picado 1913).

In recent years, herpetological collectors in the tropics have turned their attention to the bromeliaceous habitat niche, with gratifying results. The plants have been found to harbor many forms of reptiles and amphibians, some mere casual invaders of the habitat, others almost exclusively bromeliaceous (Dunn 1937; Smith 1941). Many novelties have thus been brought to light, especially salamanders of the genus *Oedipus*, and frogs of the genera *Eleutherodactylus* and *Hyla* (Schmidt 1936; Taylor 1939, 1940, 1941, 1949, etc.). Some of these forms exhibit striking adaptations to a thoroughly bromeliaceous existence (Dunn 1937; Smith 1941). No investigation of these plants has been made in Florida, as far as I am aware.

Most of the bromeliaceous plants of Florida belong to the genus *Tillandsia*. There are a number of species in the state, some small and with filiform leaves (Fig. 1), others as much as 20 dm. tall and with water-retaining leaves like those of many tropical species (Fig. 2) (Small 1933). Bromelias are widespread in the Everglades and extreme southern Florida; in some areas, such as along the Caloosahatchee River, great numbers of these plants adorn the branches and boles of the trees. Father north, scattered colonies of bromelias are encountered to about the latitude of Hernando County. Beyond this area only occassional bromelias are found, most of them being the hardy *Tillandsia tenuifolia*.

In the Florida Everglades, great stretches of country may go dry for weeks at a time. The peaty soil dries and cracks; streams vanish; ponds normally 8 or 10 feet deep become dry, dusty basins. At such times bromelias provide the only water readily available above ground. Elsewhere in the state, prolonged dry spells are not infrequent; and although larger lakes and streams may remain full of water, certain extensive habitats may be severely affected by drought. The presence of amphibians and reptiles in bromelias might, therefore, be expected under such conditions. Furthermore, many bromelias, even those whose leaves do not retain water, are a favored habitat of spiders, millipedes, beetles, moths, mosquitoes, crane-flies, and snails; one might thus expect certain species of reptiles and amphibians to invade these plants in search of invertebrate prey, as well as to find a place of concealment when not foraging.

Such indeed is the case, as the following observations indicate.

A juvenile Everglades rat snake, *Elaphe obsoleta rossalleni,* was taken from a large bromelia in March 1950, in northern Dade County, Florida. The stomach of this specimen contained two freshly-devoured green tree-frogs, *Hyla c. cinerea,* probably captured in the bromelia.

The common "chameleon," *Anolis c. carolinensis,* has been found in bromelias in practically every locality investigated. In Monroe and Dade counties, "chameleons" were taken in large bromelias, such as *Tillandsia utriculata;*

Fig. 1. A cluster of small bromelias growing on a cabbage palmetto, Marion County, Florida.

farther north, in Sumter and Marion counties, they were found in the clusters of *T. tenuifolia.*

A single Stejneger's "chameleon," *Anolis sagrei stejnegeri,* was found sleeping at night on the leaf of a bromelia at Key West, Monroe County.

The introduced Mediterranean gecko, *Hemidactylus t. turcicus,* was found on several occa-

FIG. 2. A large, water-retaining bromelia on the trunk of a pond cypress, Collier County, Florida.

sions in bromelias at Key West, Monroe County.

The green tree-frog, *Hyla c. cinerea,* was often discovered in bromelias in Monroe and Dade counties, and farther north in Sumter County. All the green tree-frogs thus found were young specimens; full-grown adults were not noted.

The squirrel tree-frog, *Hyla squirella,* is apparently a common inhabitant of bromelias wherever these plants are found. Most of the squirrel tree-frogs collected from "air-plants" were recently-transformed examples, although a few adults were noted.

The introduced Ricord's frog, *Eleutherodactylus ricordii planirostris,* was discovered on one occasion in a low-growing mass of bromelias in Dade County.

My investigation of bromelias has not been extensive; no doubt a thorough examination of these plants during a prolonged dry spell would be richly rewarding, especially in the Everglades. As yet, no form of reptile or amphibian confined to "air-plants" has been discovered in Florida; but the mere existence of a bromeliad herpetofauna of a more casual nature is of considerable interest, for such invasion of these plants may well be the first step in the development of a thoroughly bromeliaceous species.

I am indebted to E. Ross Allen of Silver Springs, and to Charles D'Andrea of Miami, for assistance in this study.

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ESTIMATION OF THE AGES OF FOREST STANDS IN THE PRAIRIE-FOREST BORDER REGION

Introduction

There has been a long felt need for some method of arriving at an estimate of the time during which particular areas have been in forest cover; particularly is this true in the prairie-forest transition region where study of climatic changes and succession demands knowledge of the history of the area under study. Two methods were tried in the course of this study: clone measurements and shade tolerance ratings. If clones of herbs represent continuous vegetative growth since an initial seed establishment, then the size of a clone divided by the rate of growth of the species should result in a minimum age necessary to attain that size. Similarly, it has long been recognized that trees differ in the degree of their shade tolerance and that this fact is largely responsible for the difference in tree composition between young woods and old established woods. It would appear, therefore, that if one could establish the relative tolerance of each species, one might, by computing the percentages of tolerant and intolerant trees in any stand, arrive at an estimate of the ecological age of the stand, and possibly even of the chronological age. Logically, the limit of this method is reached in a stand which is 100 per cent tolerant. For such a stand only a minimum age could be assigned. On the other hand, barring extreme edaphic conditions, a stand in the region of this study whose composition is 100 per cent intolerant is almost certainly a first generation stand.

In order to test these hypotheses, twenty-six stands in the prairie forest border region of Wisconsin were sampled by the author during the summer of 1947, and the stands were ranked by the tolerance method in order from the youngest to the oldest. The order of rank was then checked by comparison with data from stump rings and tree borings, and with data derived from clone measurements.

The region studied extended from the Mississippi River near Prairie du Chien in southern Wisconsin to Downers Grove, Illinois, which lies some twenty miles west of Chicago. The western part of this region lies in the Driftless Area and the eastern part within the area of the Wisconsin stage of glaciation. An attempt was made to examine at least two stands of

different types and ages in each locality, and to distribute these localities across the general border region.

Tree Data and Shade Tolerance

A modification of the point method worked out by Cottam and Curtis (1949) was chosen as the fastest and simplest method for sampling the trees in each stand. Twenty points were established at predetermined, paced intervals and the girth and species of the two nearest trees were recorded at each point, thus yielding a sample of forty trees per stand.

Because the shade tolerance of species varies regionally it was necessary to estimate the tolerance of the species as they are found within the geographical limits of the study. These tolerance estimates are presented in table I, together with the ratings of fifty-five foresters as summarized by Baker (1949) which are presented for comparison.

Table I. *Tolerance ratings of tree species*

Whitford	Baker (1949)*
Intolerant	Very Intolerant
American Elm	Aspens 85
Aspens	
Black Cherry	Intolerant
Black Oaks**	Black Walnut 60
Box Elder	Butternut 80
Bur Oak	Hickories 48
Shagbark Hickory	Paper Birch 83
White Birch	(Red Oak 32)
White Oak	(Black Oak 45)**
	Black Cherry 50
	(Ashes 38)
Intermediate	Intermediate
Black Walnut	White Oak 74
Butternut	Red Oak 59
Hackberry	Black Oak 55**
Red Maple	(Hickories 41)
Ashes	American Elm 59
Red Oak	Hackberry 100
	(Black Cherry 45)
	(Basswood 38)
	Ashes 55
Tolerant	Tolerant
Basswood	Red Maple 69
Ironwood	Basswood 46
Slippery Elm	
Sugar Maple	Very Tolerant
Yellowbud Hickory	Ironwood 67
	Sugar Maple 71

* Baker summarized the results of 55 returns of a questionnaire sent to professional foresters and the numbers following species names indicate the percentage of returns which favored each species in that category. Where considerable difference of opinion was found the second choice is shown in parentheses.

** Black Oaks include mostly *Q. ellipsoidalis* and *Q. velutina* with possibly some *Q. coccinea*. These were separated from Red Oak (*Q. rubra*), mainly by the depth of lobing of the leaves.

In order to portray the relative importance of the different tree species in each stand and in stands of different types, a composite value was derived by adding the percentage values of density, frequency, and dominance for each species. This total will be termed the "DFD index" of the species, and is the same as the "AFD index" used previously by Curtis (1947). The magnitude of the DFD index is roughly comparable to the area of the "phytograph" of Lutz (1930) for the comparison of different species in the stand. The DFD index is used here because it gives a numerical value which can be used for tables, thus supplementing the use of the phytograph to show the various aspects of the importance of any species in a stand or community.

The DFD index values for all of the species of each tolerance class were totaled for each stand. The percentage of intolerant species relative to the percentage of intermediate and tolerant species shows the degree of successional development of each stand. For convenience in handling the data the stands were separated arbitrarily into three groups on the basis of the per cent of total DFD in each stand composed of intolerant species. The group referred to as oak-hickory includes all stands in which the intolerant species compose over 75 per cent of the stand; the intermediate group represents stands having 25 to 75 per cent intolerant species; while the maple-basswood group represents stands which have less than 25 per cent of their total DFD of intolerant species.

Final ranking of the stands placed eleven of the twenty-six within the limits of the oak-hickory group, seven in the intermediate group, and eight in the maple-basswood group. The listing in table II shows that the first four of the oak-hickory stands, those which are ecologically the youngest, have 100 per cent of intolerant species; the three oldest of the stands have from 85 to 90.7 per cent of tolerant species. Only three stands had over 54 per cent tolerant species, indicating that the maple-basswood climax which has been postulated for this region is not well developed within the range of this study.

Some of the tree species[1] exhibited patterns of importance which had not been anticipated for them. As would be expected the black oak (*Quercus* spp.), bur oak (*Quercus macrocarpa*), shagbark hickory (*Carya ovata*), and cherry (*Prunus serotina*) drop rather sharply in importance from the oak-hickory type to the intermediate type; but the latter two were found to continue in minor amounts even in the maple-basswood type. White oak (*Quercus alba*), however, remains high in importance until late

[1] The nomenclature used here follows Gray's Manual, 8th edition, 1950.

TABLE II. *Comparison of data on age of stands (see text for explanation)*

Stand	Stumps and trees		Herb clones		Tolerance ratings		
	Median	Max.	Avg.	Max.	Intolerant %	Neutral %	Tolerant %
Ableman 1	95	198			100		
Madison	90	(145)	25	30	100		
Noe Woods	90	95	35	50	100		
Norway Grove		(170)	50	105	100		
Wyalusing 1					93		7
Middleton	90	(275)			92	8	
Ableman 2	85	(150)			89	11	
Lyman's 1	85	(90)	70	200	88	12	
Cazenovia 1		(150)	120	225	86	7	7
Reedsburg 1	93	120	40	80	84	14	2
Brooklyn			40	95	76	24	
Wyalusing 2	110	(130)			61	28	11
Monticello	90		45	85	56	2	42
Mortons	100	190			45	34	20
Brodhead		(140)	135	320	42	53	5
Lyman's 2		245	100	175	35	65	
Wyalusing 4		(120)			31	55	14
Wyalusing 3		(200)			25	50	25
Downers Grove		(170)	140	200	22	25	52
Beech's Woods		(120)			21	42	36
Baxter's Hollow		170			20	28	52
Coon Valley	(90)	(110)			18	73	9
Reedsburg 2			150	200+	17	29	54
Albany			120	200+	12	3	85
Cazenovia 2		150	220	425	9		91
Oakly		(175+)	125+	200+	2	9	89

in the intermediate stage and continues into the maple-basswood. Its importance in these stands is usually caused by the large sizes of a few old trees. Basswood (*Tilia americana*) enters early and increases slowly up to the late intermediate stage, when it increases more rapidly up to the rather stable value it attains in the maple-basswood type. Maple (*Acer saccharum*) and ironwood (*Ostrya virginiana*) become important only after the last stage is reached. Of note, however, is the occurrence of walnut (*Juglans nigra*) and red oak (*Quercus rubra*) which are more important in the intermediate stage than in either of the others. This would seem to support the conclusion of Sampson (1930) that the intermediate, or transition, stage is made up, not of mixtures of the dominants of both adjacent types, but of species which are secondary in the other types and here become dominant. However, this is not completely clear from the present data, and in this region basswood, white oak, and red oak serve to connect all three types and emphasize the fundamental relationship among them.

Clone Sizes and Growth Rates

A previous study (Whitford 1949) showed that many of the woodland herbs exhibit a definitely clonal distribution, i.e., appear mostly in dense local clumps, especially in their early stages of invasion. An attempt was made to ascertain the actual chronological ages of some of the clones by measuring the rates of the diameter growth of clones of *Adiantum pedatum, Athyrium filix-femina* var. *michauxii, Polygonatum canaliculatum, Smilacina racemosa, Podophyllum peltatum, Anemone quinquefolia,* and *Sanguinaria canadensis.* This was done by measuring the annual rhizome growth and arriving at an estimate of the average yearly radial growth. Then the age of each clone was estimated by dividing its diameter by twice the average radial growth of the species. Rhizome growth was measured by starting at the aerial stems or leaves of the current year and following the rhizome back, digging and washing the largest pieces obtainable, and thereafter inspecting the material to determine what exterior morphological character might indicate the extent of one year's growth. Such species as *Smilacina racemosa, Polygonatum canaliculatum,* and *Podophyllum peltatum* show obvious scars at rather uniform intervals where the aerial branches of each year arise. In such plants as *Adiantum pedatum* and other ferns which produce more than one leaf per year it is much

more difficult. However, at fairly regular intervals the rhizome is somewhat constricted and the leaf bases of old leaves are farther apart. These points are then taken to be the ends of successive years of growth. Each intact piece of rhizome was then measured and the total years and total length recorded. For example: eight sections of Adiantum from one stand gave a total of 47 years and 37 inches in length, resulting in a growth rate of approximately 0.8 inch per year. In some cases each year was measured separately, but none have thus far been checked in enough different sites and over enough years in each for a statistically valid analysis of the variation. Preliminary data for several species are summarized in table III.

TABLE III. *Rates of rhizome growth for some clonal species of forest herbs*

Species	Avg. inches per year	Years per 10 feet diameter (approx.)
Adiantum pedatum	0.79	80
Athyrium filix-femina var. *michauxii*	0.73	85
Smilacina racemosa	0.94	70
Polygonatum canaliculatum	1.38	45
Anemone quinquefolia	0.61	100
Podophyllum peltatum	5.38	12
Sanguinaria canadensis	0.26	230
Hydrophyllum virginianum	0.96	65

Most of the species selected for this work ordinarily do not become established except under the protection of forest trees and, therefore, the ages of clones of these species would be an approximation of the minimum ages of the stands in which they appear. In mature stands the clones tend to become so large and broken up that they cannot be readily identified or measured; thus age in terms of actual years is almost impossible to derive in the oldest stands of the region, although the very existence of these broken clones gives evidence of the maturity of the stands.

Stump Records

An additional check which served to show at least the minimum age of many stands was obtained by counting the annual growth rings of tree stumps. It had been hoped that age-diameter curves could be constructed from which the approximate ages of standing trees might be calculated, but this did not prove feasible, except for the white oaks. The white oaks proved to be relatively uniform in any one age class, but in contrast the black oaks were limited mainly to one age group and the variation of diameter of these even-aged trees was very high so that no curves could be constructed. The mere fact that they are even-aged is often significant; however, the conclusion (Gates and Nichols 1930) that in all-aged virgin stands there is a good correlation between age and diameter probably is valid for those conditions, and appears to be valid for the white oaks in the range of the present study.

Discussion

In table II the twenty-six stands used in this study are listed in order of increasing maturity on the basis of the tolerance ratings. The data from the other methods are presented on the same table for purposes of comparison. The data from stump records and standing trees appear to show no significant difference between younger stands and mature stands because of the lack of accurate estimates from the more mature stands. Since too little data were accumulated in this study for reliable estimates of age for any species except white oak the only age estimates which could be made in old mixed stands were those of the oldest standing white oaks. On the other hand, most of the stands which were composed largely of oaks were found to be essentially even-aged, and for these stands the median age of trees in the dominant age group could be calculated. These ages are given in the first column for stands where this applies, and are expressed to the nearest 5 years except for one stand where considerable accurate data warranted the use of an exact median age.

The second column gives the age of the oldest tree noted in each stand, which is shown in parenthesis if estimated; otherwise it is the actual record from the oldest countable stump. It should be noted that in most of the now closed stands which were recorded about 100 years ago as oak opening by the surveyors these maximum ages represent trees of the original oak opening which still show characteristics of open-grown trees (see Cottam 1949). Since the stands which were actually oldest and were of maple-basswood type 100 years ago had few if any of such trees or countable stumps the recorded maximum for them is often lower than that of younger stands. Also, in these all-aged stands if an average or median age had been feasible to obtain, the average age based on the sample of trees 4 inches d.b.h. and over would probably be lower than that of younger but even-aged first generation stands. Such data of course are obviously limited to the life span of the trees, and for stumps to the period before decay leaves them uncountable; a practical maximum of, say, 300 years here, so that the method is useful for checking the earlier stages of forest succession but would fail to separate mature stands of more than 300 years duration on a particular site.

The study of clone sizes and growth rates yielded interesting data which, though rather highly variable, are felt to be definitely correlated with the stand ages. Where possible three

of the largest clones of each species used were measured in each of 15 stands and the age was estimated therefrom as previously described. In the summary table an average of these ages is given in the first column under clone sizes and the oldest or maximum age for any of these species in the second column. Since these figures are all based on estimates they were rounded in the table to the nearest five years. The species used rarely become established without the protection of forest cover, at least in this region, so that the mean age of, say, a dozen of the oldest clones present should indicate the minimum time since the forest cover appeared.

This method, like the tree sizes and stump records, has an upper limit of usefulness in that the clones tend to become too large and fragmented to be identified as such. For purposes of computation the large broken clones which were listed as indefinite in field notes were added as 200 + years each, so that the most mature stands, in which few definable clones were found, are recorded here with lower minimum ages than stands which by other methods were younger. At the other extreme in the youngest stands the complete absence of some of these woodland species is undoubtedly significant, but is omitted from the table to avoid over-crowding. Within these limitations, however, the clone data appear to corroborate the other data, inasmuch as the average ages show a definite increase with the increase in importance of tolerant tree species. The few rather high clone ages, especially maxima, in ecologically younger stands are probably explainable on the basis of a long presettlement history of oak opening or thin woods, during which some few forest species may have become established locally in the most favorable shaded spots.

Summary

Two new approaches to the problem of how long a forest may have existed on a given site were explored. While the findings are still preliminary it is believed that they have possibilities worthy of note. Clone ages for forest herbs which reproduce mainly by vegetative means may be derived from the size of a clone and the rate of growth of the species, giving an approximate minimum age of the stand. By ranking trees in three tolerance classes and calculating the percentage of DFD totals for each class in each stand, a ranking of stands in order of ecological age is possible. The results of these two methods are compared in the summary table with the minimum ages determined from standing trees or stumps. Granting the limitations mentioned, there is rather good agreement of results and it is felt that both methods are worthy of further work. Probably a refinement of the tolerance method and more adequate sampling are in order to prove its validity and increase its accuracy and usefulness. More data on the cloning and clonal growth rates of all forest species and on their ecological range are needed to increase and define the accuracy and usefulness of this method. No such information was found when this study began; however, the results of this preliminary check indicate that such knowledge is a logical objective of ecological as well as morphological study.

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VERTICAL DISTRIBUTION OF *STENTOR COERULEUS* IN RELATION TO DISSOLVED OXYGEN LEVELS IN AN IOWA POND[1]

While conducting routine periodic dissolved gas and alkalinity observations in connection with a fish population study in an Iowa farm pond, the writer's attention was attracted to the apparent relationship between the vertical

[1] From Iowa Cooperative Fisheries Research Unit, Project 42, sponsored by the Industrial Science Research Institute of Iowa State College and by the Iowa State Conservation Commission.

distribution of *Stentor coeruleus* Ehrenberg and water strata containing low concentrations of dissolved oxygen. Birge and Juday (1911) found *S. igneus* occupying a stratum of water containing little or no free oxygen in Beasley Lake, Wisconsin, during the entire summer of 1909. Some 200 specimens per liter were reported found at one depth where the water contained no free oxygen. Noland (1925) collected *S. roeseli* from natural waters with dissolved oxygen conditions ranging from 2.4 to 8.3 cc./liter (3.4 to 11.8 ppm.) and *S. igneus* from strata containing 6.8 to 8.0 cc./liter (9.7 to 11.4 ppm.). The same author reported *S. coeruleus* and *S. roeseli* living in the laboratory in waters exhibiting 0.4 and 0.1 cc. of dissolved oxygen per liter (0.5 and 0.1 ppm.), respectively. The writer has been unable to locate any record of as clear-cut a relationship between dissolved oxygen and the distribution of Stentor as is here reported.

McFarland's Pond is a relatively new and moderately fertile 7 acre artificial pond situated in a protected valley near Ames, Story County, Iowa. Maximum depth in the pond is 6.5 meters and approximately one-third of the impoundment has a depth greater than 4.5 meters. The topography of the basin is such that the pond becomes thermally stratified and develops a thermocline during the summer months. No higher submergent aquatic vegetation is present except at the shore line, although algal growth is particularly abundant in mid- and late summer.

Water samples were collected in 250 ml. glass bottles by means of a Juday bottle at one meter depth intervals once each week during the period August 1949 to early April 1950 inclusive. The terms "abundant," "few," and "none were arbitrarily used for recording the relative abundance of Stentor contained in the samples. The population was considered to have "abundant" numbers when a 250 ml. sample of water contained more than 15 of the animals. "Few" referred to the presence of 1–15 of the organisms per bottle.

"Abundant" quantities were recorded at least once in each month of the observation period with the exceptions of November, March, and April, but a "few" were always to be found at some depth in the pond.

When water strata containing different concentrations of dissolved oxygen were present, greater numbers of Stentor could usually be found at those levels in which the quantity of oxygen was reduced. As summarized in table I, "abundant" Stentor were found on 17 occasions and only in water containing dissolved oxygen within the range of 0.1–2.8 ppm. The population density in each case decreased from "abundant" to "few" or "none" within vertical distances of less than one meter above and below the stratum concerned. Rather marked differences in oxygen concentrations were usually also noted within these vertical distances. "Few" organisms were recorded 78 times in water containing 0.0–11.4 ppm. of dissolved oxygen. However, the pond was in the process of "fall overturn" or was well oxygenated throughout in each of the 29 instances where the dissolved oxygen concentrations were greater than 5.4 ppm.

The distribution and abundance of these animals seemed to have been little influenced by dissolved carbon dioxide, alkalinity, pH, temperature, or depth of sample. Table II lists the ranges of these factors within which Stentor were found.

TABLE I. *Distribution of Stentor in relation to dissolved oxygen*

Ppm. dissolved oxygen	Number of times Stentor population observed		
	"None" per sample	"Few" per sample	"Abundant" per sample
0.0	9	2	0
0.1– 0.5	8	14	5
0.6– 1.0	0	5	6
1.1– 1.5	1	1	3
1.6– 2.0	0	3	2
2.1– 2.5	1	2	0
2.6– 3.0	2	2	1
3.1– 4.0	5	10	0
4.1– 5.0	4	8	0
5.1– 6.0	9	3	0
6.1– 7.0	9	10	0
7.1– 8.0	6	6	0
8.1– 9.0	3	0	0
9.1–10.0	4	5	0
10.1–11.0	1	5	0
11.1–12.0	1	2	0
12.1–12.5	1	0	0

TABLE II. *Distribution of* Stentor coeruleus *in relation to some water conditions in an Iowa pond*

Population density of Stentor	Range of factors				
	Water temperature (° C.)	Free CO_2 in ppm.	Total carbonates in ppm.	pH	Depth in meters
Abundant	3 –26	4–21	150–225	7.0–7.7	0.08–5.0
Few	2 –18	3–24	52–282	6.8–7.6	0.08–5.0
None	0.5–26	0–34	40–230	6.8–8.4	0.08–6.0

In spite of the tendency to be abundant only under nearly anaerobic conditions, Stentor appeared able to readily adapt itself to changing environmental conditions. A large number of specimens, taken on February 17 from a pond stratum containing only 0.7 ppm. of dissolved oxygen at a temperature of 3° C., was brought

into the laboratory and allowed to warm to room temperature (20–25° C.). The organisms were then put in wide mouth glass jars and placed near a north window. Sprigs of *Anacharis canadensis* were added to two of the jars, but the third was left undisturbed except for the addition of tap water to make up for losses from evaporation. After two weeks in the laboratory the Stentor populations in the three jars were somewhat reduced in numbers, but the remaining specimens appeared to have increased in size. Twenty of the Stentor specimens, measured soon after being brought in from the pond, had an average length extended of 0.832 mm. Twenty specimens taken at random from the jars after two weeks in the laboratory averaged 1.328 mm. in length extended. Though a dilute solution of methocel was used to reduce the animals' swimming activities while measurements were being made, the methocel did not seem to interfere with normal extension until drying began to occur. Dissolved oxygen concentrations in the jars containing *Anacharis* were 6.9 and 6.0 ppm., whereas 3.4 ppm. were found in the container which lacked this plant material. No difference in relative abundance or size was detected between the populations of the individual jars.

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THE OCCURRENCE AND DISTRIBUTION OF HEMLOCK IN ALABAMA[1]

The first record of *Tsuga canadensis* (L.) Carr. in Alabama is cited by Mohr (1901) from Clear Creek and East Fork Creek in Winston County. These localities are near the southwestern extremity of the Cumberland Plateau and are in a region called the Warrior River Tableland by Mohr and the Warrior Basin by Johnston (1930) and Fenneman (1938). It is actually a deeply dissected plateau which is drained chiefly by the Warrior River and we will refer to it as the Warrior Plateau.

Harbison (1902) found the tree growing along Bryan Creek on Sand Mountain in the northeastern part of the state. This creek has cut a deep gorge known as Pisgah Gulf in the central portion of Jackson County. Stations for the species in Franklin, Marion, and Jefferson counties are listed by Harper (1919). All of these localities are underlain by rocks of the Pottsville formation.

Mr. R. L. James discovered hemlock growing along Fox Trap Creek in southeastern Colbert County (Harper 1943) on soils derived from Hartselle sandstone. The comparative resistance of this sandstone has produced an area with higher surface levels than those which are underlain by the limestones of the Tennessee Valley on the north and the Moulton Valley on the south. The area where Hartselle sandstone outcrops, which is called Little Mountain, lies in an east-west direction and is separated from the Warrior Plateau by the Moulton Valley.

Although hemlock is common on Lookout Mountain in northwestern Georgia (Duncan 1941: 49), extensive field work on the Alabama portion of the mountain has failed to discover the plant in that region of the state.

The writers began exploration of northern Alabama in the summer of 1949 and many stations for the species have been added to those previously discovered. The known range of the plant in the state has been extended northward, westward, and southwestward and four counties have been added to the list of those in which it occurs.

The Pisgah Gulf locality remained the only one known for the species on Sand Mountain until 1949 when the plant was found on the western fork of Dry Creek (fig. 1). Thus, the species exhibits a marked disjunction on Sand Mountain. Southwestward from Pisgah Gulf, hemlock first occurs in Cullman County where a few trees are known near an unusual rock formation which is called "The Penitentiary." Six or eight miles westward from this locality, the plant becomes abundant in Winston County and it is also abundant in Marion County which adjoins Winston County on the west. In addition to the Cullman County station, recent field work has added Lawrence (Kinlock Falls and King Cove), Walker (Lost Creek and Duncan Creek), and Lamar (Stuck's Springs) counties to those in which hemlock is known to be native. The Lamar County locality is but twelve miles from the Mississippi border.

[1] Field work was supported by a grant to Harvill from the Research Committee of the University of Alabama.

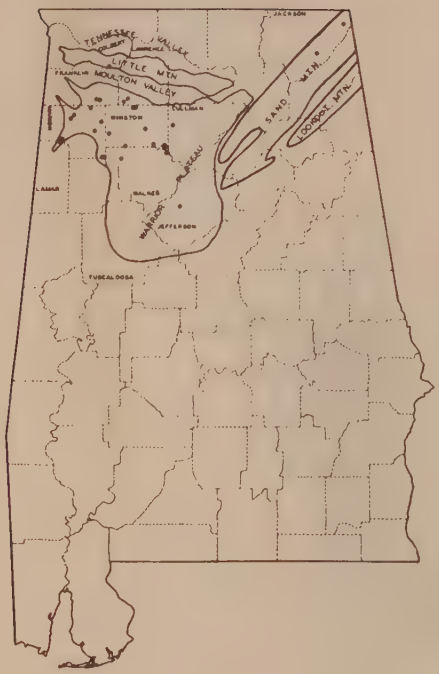

FIG. 1. Map of Alabama showing physiographic regions and stations for hemlock. Each dot represents a collection made by the writers. Specimens are preserved in the herbarium of the University of Alabama.

Among the interesting associates of hemlock in Alabama are such cryptogams as *Asplenium montanum* Willd., *A. pinnatifidum* Nutt., *Diphyscium cumberlandianum* Harvill (Harvill 1950), *Mnium punctatum* Hedw., *Rhodobryum roseum* (Hedw.) Limpr., *Tetraphis pellucida* Hedw., *Thelypteris pilosa* (Mart. and Gal.) Crawford (Crawford 1950), *Trichomanes boschianum* Strum, and *T. petersii* Gray. Of the phanerogamic plants of interest we should list *Orchis spectabilis* L., *Juglans cinerea* L., *Betula lenta* L., *Trautvetteria caroliniensis* (Walt.) Vail, *Thalictrum clavatum* DC., *Boykinia acontifolia* Nutt., and *Heuchera parviflora* Bartl. var. *rugelii* (Shuttlw.) Rosend., Butt., and Lak.

It has been demonstrated that the floras of the southern states had many species in the Pleistocene which are now limited to more northern latitudes (Brown 1938; Potzger and Thorp 1947) and we may infer that climatic conditions, over a great part of Alabama, were more suitable for the growth of hemlock than they are today. We would hesitate to suggest, however, that the plant extended far beyond its present limits because edaphic conditions may have precluded its occupation of areas farther south.

The macroclimates of the Warrior Plateau, where the southern limits of the range of hemlock occurs, do not differ much from those of neighboring regions. This is shown in table I by the records for Florence, Madison, Hamilton, Fayette, and Tuscaloosa. Data for the table have been taken from Emigh (1941: 751–760). March is the wettest month and September is the driest month at all of these stations.

Preliminary evaporation data taken by means of the porous cup atmometer suggest that there may be botanically significant differences in the microclimates, at least in the evaporation regimes, between the places where hemlock occurs and the other areas. During the months of June and July, the average daily loss of water from an atmometer placed in the shade of a hemlock at the bottom of King Cove (Lawrence County) was 4.6 cc, whereas an atmometer in the shade of oaks and pines at the top of a ridge near King Cove lost 10.3 cc per day. It is of interest that during the same period, atmometers in somewhat comparable situations in the Black Belt (9.5 miles west of Selma, Dallas County) and on the Gulf Coast (near Fairhope, Baldwin County) lost approximately 25 cc and 26 cc per day, respectively.

From these data, it is believed that the high humidity in the areas where hemlock grows on the Warrior Plateau has played an important rôle in the persistence of the species in the region.

TABLE I. *Macroclimatic data for seven Alabama stations*

Station	Altitude in feet	Temperature		Avg. annual precipitation in inches
		Avg. for Jan.	Avg. for July	
Madison (Tenn. Valley)	573	43.4	80.1	52.47
Florence (Tenn. Valley)	450	42.3	79.7	52.59
Hamilton (Warrior Plateau)	498	43.2	78.8	50.13
Fayette (Inner Coastal Plain)	359	43.2	81.1	57.62
Tuscaloosa (Inner Coastal Plain)	146	45.8	81.5	54.07
Selma (Black Belt)	147	49.9	81.7	50.29
Silver Hill (Gulf Coast)	250	53.8	80.9	62.68

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THE INTERNATIONAL OLYMPIC GAMES AND THE INFLUENCE OF CLIMATE ON HUMAN ENERGY

The International Olympic Games are famous and almost every nation of the world sends its teams, composed of its best athletes, in the hope that they will distinguish themselves in the various sports which figure on its program, and bring home some of the international honors. The results of the competitions are expressed in points (extraofficially) and the quantity of the points won by the representatives of the various countries offers a good basis for a statistical research on the influence of climate on the activity and constitution of man. My first investigation in this respect, made in 1925 and sponsored by Ellsworth Huntington (Hoxmark 1925), was reproduced later in *The Literary Digest,* September 12, 1925, and discussed in books and journals all over the world.

The Commission for the International Olympic Games included winter sports in the games celebrated in 1920 and afterwards. The early paper treated the relations found between the annual mean temperatures for the countries taking part in the games and the success of their athletes at Antwerp (1920) and Paris (1924), while the present includes Berlin (1936) and London (1948), taking into account, as far as possible, the demographic variations operating during the past years.

In order to obtain adequate values whereby one can measure the effects of climate, the first step is to divide the numbers of inhabitants by the points won. This operation shows how many people there are per point in the various countries. The next step is to calculate the index numbers which figure in column A (see

TABLE I. *Mean of index numbers of points obtained, in relation to population, at Antwerp, Paris, Berlin, and London, and the mean annual temperature*

Rank	Country	A Mean of index numbers	B Mean annual temperature	
			° C.	° F.
1	Norway	1.07	3.8	38.7
2	Finland	1.22	3.1	37.6
3	Sweden	1.43	5.1	41.2
4	Switzerland	2.69	8.6	47.5
5	Denmark	4.02	7.2	45.0
6	Holland	5.51	8.7	47.7
7	Hungary	5.93	9.7	49.5
8	Austria	7.73	9.6	49.3
9	Canada	10.41	4.6	40.3
10	Argentina	11.98	13.5	56.3
11	France	12.07	11.7	53.1
12	United States	14.05	10.6	51.1
13	Great Britain	15.78	9.6	49.3
14	Italy	15.92	15.2	59.4
15	Belgium	20.00	9.1	48.4
16	Australia	39.61	17.2	63.0
17	Union of S. Africa	41.53	16.4	61.5
18	Czechoslovakia	52.98	8.3	46.9

TABLE II. *The International Olympic Games, Berlin, 1936*

Rank	Country	Index numbers	Points obtained
1	Norway	1.0	135
2	Finland	1.2	152
3	Esthonia	1.3	39
4	Sweden	1.9	154
5	Switzerland	2.2	90
6	Austria	3.2	98
7	Hungary	3.3	130
8	Holland	3.8	101
9	Germany	5.3	595
10	New Zealand	7.7	10
11	Denmark	9.0	19
12	Canada	10.9	45
13	Latvia	11.3	8
14	Czechoslovakia	12.9	55
15	United States	14.2	396
16	Argentina	14.8	39
17	Italy	15.3	130
18	France	16.3	121
19	Great Britain	20.6	102
20	Egypt	21.1	31
21	Japan	41.7	104
22	Turkey	55.9	13
23	Belgium	64.8	6
24	Poland	64.9	24
25	Union of S. Africa	65.4	5
26	Mexico	87.7	9
27	Portugal	104.6	3
28	Australia	105.0	3
29	Yugoslavia	131.4	5
30	Rumania	173.6	5
31	Philippines	190.8	3
32	India	1664.3	10

TABLE III. *"Short list of the twenty best performances at The International Olympic Games, London, 1948*

Rank	Country	Index numbers	Points obtained
1	Sweden	1.00	375.5
2	Norway	1.28	130
3	Switzerland	1.29	187
4	Finland	1.36	158
5	Denmark	1.87	129
6	Hungary	2.90	185
7	Holland	4.14	118
8	Austria	4.69	80
9	Australia	4.93	87
10	Belgium	5.30	86
11	Canada	8.15	79
12	France	9.26	249
13	Czechoslovakia	9.42	74
14	Union of S. Africa	10.73	35
15	Turkey	11.76	73
16	United States	12.60	596
17	Italy	12.70	190
18	Argentina	13.73	62.5
19	Great Britain	15.41	174
20	Mexico	27.20	35.5

table I). To this end the smallest number of inhabitants per point is called 1.00, a position attained by Norway on three occasions and by Sweden once, the other countries ranking accordingly. The index numbers afford an easy way of estimating how far any nation deviates from the best result, or 1.00. The mean annual temperature (column B) has been added to the table. Tables II and III give the later results.

The relations between athletic prowess and thermal conditions are shown graphically in figure 1. The sequence of the index numbers (mean of four Olympics) shows a positive influence of temperature on the skill of the competitors in the contests, and consequently on the

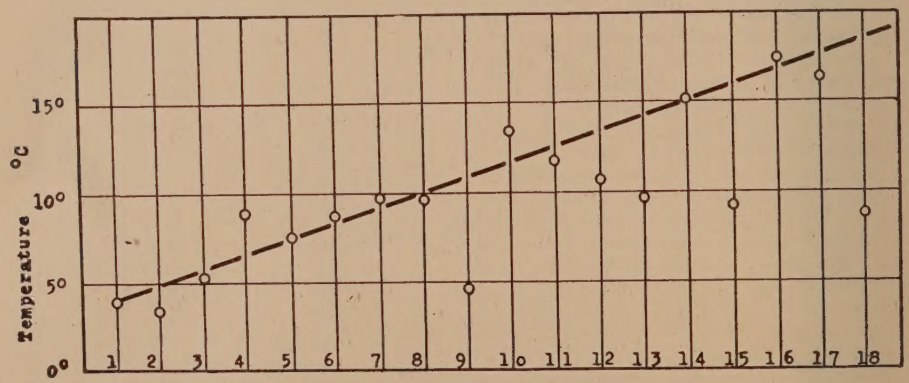

FIG. 1. Correlation between average annual temperature and the mean index numbers of points obtained in the Olympic Games of 1920, 1924, 1936 and 1948.

peoples they represent. Wars have had, apparently, a slight negative effect on some nations involved in the world conflicts, and others seem to lag permanently behind, possibly because they are practising, by preference, sports not admitted by the programs of the games, even though this cause can not fully explain the anomaly. It is likely that other, deeper reasons exist, but in this study we will not go too far into the exceptions from the average law of the correlation between physical energy and thermal conditions.

At the end of the paper published in *Ecology* twenty-five years ago, the following remarks were made: "It will be interesting to watch future Olympics in order to see whether the data in diagrams like the one here given (for 1920 and 1924) become more widely dispersed or gather more closely in the neighborhood of the line of dashes, as they must if temperature is really a controlling factor in physical strength and athletic prowess." The present diagram, representing the mean results for the later Olympics, averaged with those obtained in the first case, is a reply to the question.

The northernmost countries, Norway, Finland, and Sweden, are continuing in the van, followed by Switzerland and Denmark. (Switzerland temperatures were taken from lowland stations, but the real values may be lower as the country is extremely mountainous.) It may be that the athletes coming from higher latitudes and cooler climes where the air contains a slightly higher percentage of oxygen and nitrogen than farther south, and those from mountain regions, possess a greater mean lung capacity and, therefore, are better adapted for making violent physical exertions during shorter or longer periods.

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BOOK REVIEWS

Anatomy of the Dicotyledons [1]

The first question which the present-day plant ecologist will ask is "Why should I be interested in a book on anatomy?" This is, of course, a natural reaction. However, it is only fair to look beyond the title, without examining too closely our hypothetical ecologist who has revealed, by his question, a lamentable lack of interest in autecology. Out of simple justice to Drs. Metcalfe and Chalk their own statement of some of their aims in producing this massive and monumental work should be examined. Not only has the book "been written mainly so as to emphasize the taxonomic and phylogenetic value of histology," but "some attention has . . . been devoted to ecological and developmental anatomy" as well.

The ecologist will approach this great reference work much as he did its predecessor, Solereder's "Systematic Anatomy of the Dicotyledons," namely, as an inventory of the currently available information concerning the vegetative anatomy of the Dicotyledons. Before the reader refers to the treatments of the individual families, the long and excellent Introduction deserves careful reading. The writers here present their terminology and an evaluation of the more recent research dealing with phylogenetic and systematic anatomy. Fortunately the terminology is straightforward and in keeping with that being used by contemporary descriptive anatomists. In their discussion, the authors repeatedly weigh anatomical characteristics from the point of view of their stability and corresponding usefulness in taxonomy and phylogeny. Their viewpoints and the information which they present are well worth critical appraisal by the ecologist. The experimental ecologist with morphological leanings will be able to ferret out suggestions for new experimental plants and problems. May your reviewer here emphasize his hope that the experimentalist will interpret his anatomical observations on a sound ontogenetic basis! If the ecologist is a devotee of adaptational morphology perhaps he will be stimulated by Metcalfe and Chalk to re-appraise the phylogenetic factor in the interpretation of his observations.

The information in the body of the book is gathered together by families, their delimitation being modern. The arrangement of the families follows the Bentham and Hooker system, a rather unfamiliar one to botanists of the United States, but this is of relatively little importance, since the forty-two page index serves the reader as an admirable guide. Under each family there is at the start a Summary of the anatomical conditions to be found in it, followed by a more specific consideration of *Leaf, Axis, Root, Anomalous Structure, Physiological or Ecological Anatomy, Taxonomic or Phylogenetic Notes, Economic Uses, Genera Described,* and *Literature.* Key anatomical terms are in bold-face which facilitates search for information. Illustrations largely are diagrammatic drawings, in which a standard set of conventions is followed. The treatment of the text is condensed, but is accompanied by an abundance of literature references. Some 2,500 citations form the basis for the information drawn from the literature since 1908 when the English edition of Solereder was published; the reader is referred to Solereder for a digest of the literature before that date. The work is far more than a summary of the literature, the descriptions of secondary xylem of the stem being based primarily on the collections of the Imperial Forestry Institute at Oxford supplemented by those of the Yale School of Forestry. The Jodrell Laboratory of the Royal Botanic Gardens, Kew, seems to have been the center of original investigation on the anatomy of other organs and tissues. Thus a vast amount of original work has entered into the information presented.

No keys are to be found, but the "Lists of families in which certain diagnostic features occur" at the end of volume two serve as an approximate equivalent. The diagnostic features are distributed as sub-headings under the following main headings: *Hairs; Leaf; Stem; Crystals, cystoliths and cristarque cells; Internal secretory structures; Wood.* This is followed by a section on *Distribution* and another on *Habit.* Finally there is an "Appendix I" which summarizes "Distribution of cell dimensions, etc., in dicotyledonous woods."

One's first reaction to these volumes is based simply on their physical appearance. The excellent paper and typography are tributes to the usual high standards of the Oxford University Press which are maintained in spite of shortages. Even more striking is its recognition that as a University Press it is its privilege and duty to publish major scholarly works at reasonable cost—let the University Presses of the United States look to their laurels!

It is most reassuring to find a publication of this caliber appearing in these troubled times—a publication which was contracted for in 1938 and pushed on to completion in spite of the psychological and physical hazards current in a country hard hit by war and its severe economic aftermath.

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[1] **C. R. Metcalfe and L. Chalk, with the assistance of M. M. Chattaway, C. L. Hare, F. R. Richardson, E. M. Slatter.** Anatomy of the Dicotyledons. *Leaves, Stem, and Wood in Relation to Taxonomy with Notes on Economic Uses.* Two vols. Roy. 8vo., pp. i–lxiv + 1–1,500, with 317 text-figures. Oxford University Press, London and New York, 1950. £6. 6s. and $25.00.